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Proceedings of the Fourth Lake States Forest Tree Improvement Conference

LAKE STATES FOREST EXPERIMENT STATION
FOREST SERVICE
U. S. DEPARTMENT OF AGRICULTURE

FOREWORD

The Lake States Forest Experiment Station* is glad to facilitate the work of the Lake States Forest Tree Improvement Committee in encouraging and coordinating forest genetics activities in this region. We are happy, therefore, to publish this Proceedings of the Fourth Lake States Forest Tree Improvement Conference, as we did for the preceding three conferences in 1953, 1955, and 1957.

M. B. Dickerman, Director

Lake States Forest Experiment Station

* Maintained at St. Paul 1, Minn., in cooperation with the University of Minnesota.

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ACKNOWLEDGMENTS

The Fourth Lake States Forest Tree Improvement Conference was the highlight of activities of the Lake States Forest Tree Improvement Committee for the past biennium. It provided another means for the Committee to encourage and coordinate forest tree improvement activities in the region. Through the Proceedings the record of the Conference becomes available to all, and the Committee hereby expresses its appreciation to the Lake States Forest Experiment Station for publishing it.

It takes a lot of work to arrange and conduct a conference such as this, and we want to thank all those who helped do so. Stephen H. Spurr was in charge of arrangements; he was assisted by Jonathan Wright, Scott Pauley, F. J. Hodge, Paul Rudolf, and your Chairman. The University of Michigan provided meeting facilities and handled many of the arrangement details. Our sincere appreciation is offered to those who participated in the program, and to those who came from other regions to meet with us. The success of the conference is a tribute to all three: those who planned it, those who presented material, and those who made up the receptive audience.

The Lake States Forest Tree Improvement Committee

W. H. Brener, Chairman

CONTENTS

	Page
Principles of Mendelian genetics applicable in forestry, Erich Steiner	1
Applications of population genetics to forest tree breeding, John E. Grafius	8
Role of introduced species in forest genetics, Stephen H. Spurr	10
The ecotype concept and forest tree genetics, Hans Nienstaedt	14
Individual tree selection in forest genetics, Jonathan W. Wright	25
Species and racial hybridization in forest genetics, H. B. Kriebel	33
Mineral nutrition of plants, A. G. Norman	44
Current forest tree improvement research in the Lake States, Paul O. Rudolf	46
Industry's part in forest tree improvement research in the Lake States, J. W. Macon	48
Activities of the Lake States Forest Tree Improvement Committee, Paul O. Rudolf	51
Resolutions	53
Field trip highlights	54
List of those registered at the conference	55
Common and scientific names of tree genera and species mentioned in text	58
List of publications previously issued for the Lake States Forest Tree Improvement Committee (back cover)	60

PRINCIPLES OF MENDELIAN GENETICS APPLICABLE IN FORESTRY

by Erich Steiner[1/]

It is well known that the variation exhibited by living things has two components, one hereditary, the other environmental. One objective of any crop improvement program is to organize hereditary variability into combinations of maximum economic value. To attain this objective, it is first necessary to understand how the hereditary traits of an organism are determined and how these traits are transmitted from generation to generation.

Our knowledge of the principles of heredity has come largely from a relatively small number of organisms, which, because of their short generation time, ease of culture, and extensive variability, are ideally adapted for genetic studies. Among these are representatives of widely different groups which, nevertheless, have been shown to possess the same basic hereditary mechanism. The universality of the fundamental principles of heredity stands as one of the major unifying concepts of biology. We have every reason to believe, therefore, that in its basic features the hereditary mechanism of forest trees conforms to that of organisms whose genetics have been much more intensively studied.

The Particulate Theory of Heredity

Insight into the hereditary mechanism can be gained by crossing two strains that show contrasting forms of a particular hereditary trait and following this trait through several generations. Let us assume that we have two strains of a tree species that differ appreciably in the height attained by the mature individuals. Each of these strains breeds true. When the tall and short strains are crossed, all of the offspring prove to be tall. If the trees of the first or F_1 generation are crossed, the next generation (F_2) is composed of both tall and short individuals in the proportion of approximately 3 tall to 1 short. The kind and frequency of offspring in such a series of crosses can be explained if we assume the following:

(1) The height character in this species is controlled by a particle or unit. Such a hereditary determiner is called a gene.

(2) A particular kind of gene--for example, that controlling height--may exist in one or more alternative states, called alleles. Each allele produces a different form of the trait that the gene controls; thus in the above cross one allele of the height gene produces a tall tree, while the other produces a short one.

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(3) Each individual carries two representatives of each kind of gene. Although only one of these is passed on to a particular offspring, each of the two has an equal chance of being transmitted.

(4) The reappearance of the short trees among the progeny of the second generation is evidence that the short form is not lost in the first generation, but merely masked. Short is thus <u>recessive</u> to tall, which is the <u>dominant</u> character.

These assumptions are diagrammed below:

Parents Tall tree X Short tree

●● 00

First generation (F_1) Tall trees

●0

Tall tree (F_1) X Tall tree (F_1)

●0 ●0

Second generation

	●	0
●	●●	●0
0	0●	00

Tall trees Short trees

1 ●● 2 ●0 1 00

If this scheme is correct, the breeding behavior of each of the individuals in the second generation should be predictable. One-third of the tall trees will breed pure, while two-thirds will breed like the F_1 offspring. The short individuals will all breed true. When such tests are carried out, the predictions are confirmed and the validity of the hypothesis is supported. The concept that the hereditary traits of an organism are determined by particles (genes) which are transmitted from generation to generation without loss of integrity was first developed by Mendel and is known as the Mendelian or particulate theory of heredity.

With respect to the crosses which we have used to derive the concept of a particulate hereditary determiner, two additional points are worthy of emphasis. Although dominance of one allele over another may often occur, it is not by any means always complete nor a universal phenomenon. When two alleles are brought together in an individual, whether dominance will occur or whether each allele will express its own effect cannot be predicted. A second point to be noted is that the first-

generation offspring are uniform in their hereditary constitution. This provides a basis for the generalization that the first-generation offspring between two pure breeding strains are composed of a single hereditary type.

The Chromosome Theory of Heredity

If these units, called genes, exist, where in the organism are they located? What is their physical basis? An understanding of the details of reproduction in an organism helps to answer this question. The link between one generation and the next is found in the gametes, sperm and egg, which fuse to form the zygote from which the new generation develops. In the seed plants the sperm are brought to the egg by the pollen tube. Frequently the male contribution to the zygote consists of only a sperm nucleus with little or no cytoplasm, the cytoplasm of the zygote being derived from the maternal parent. Yet it is clearly apparent from breeding experiments that with few exceptions the male contributes as much as the female to the heredity of the offspring. Thus it follows that the genes must be carried in the nucleus and not by the cytoplasm of the cell.

The primary constituents of the nucleus are the chromosomes; when a nucleus divides, the chromosomes are duplicated and precisely apportioned in kind and number to the daughter nuclei. The heredity of an organism is remarkably stable within limits. This stability must be related to the precision in chromosome duplication and distribution when new cells identical in heredity are formed from old, and suggests that the genes are carried by the chromosomes.

A study of the chromosomes through the reproductive cycle reveals a direct parallel between chromosome and gene behavior. Each parent possesses two sets of chromosomes; when the spores are formed which give rise to the gametes, a reduction division or meiosis occurs so that each spore, and therefore, each gamete, receives only one set. Meiosis allows the equal distribution of the chromosomes to the spores (gametes), one of each kind of chromosome occurring in each gamete. When the sperm and egg fuse, two sets of chromosomes are brought together in the zygote. If one assumes that the gene is located on a chromosome, the transmission of the hereditary unit can be accounted for in terms of the transmission of the chromosome.

Independent Assortment

In studying the heredity of an organism we must inevitably deal with more than a single hereditary character at a time. Let us assume that another pair of contrasting forms of a trait is determined by a pair of alleles residing on a second pair of chromosomes. If we follow the alleles as well as the chromosomes through the reduction division, we find that the particular combination of genes which a gamete receives

will depend upon the orientation of each pair of chromosomes during meiosis, as shown in Figure 1. Since each pair of chromosomes assumes independently and purely as a matter of chance one or the other of the two possible orientations, each of the combinations of the chromosomes and their alleles occur with equal frequency. For a particular pair of alleles, A and a, the probability of a specific allele occurring in a certain gamete is $\frac{1}{2}$. The same probability holds for another pair of alleles on a different chromosome pair. Since each pair of chromosomes becomes oriented independently of the others, when we consider two pairs of alleles simultaneously, the probability of obtaining a particular combination in a gamete, e.g. AB, is $\frac{1}{2}$A x $\frac{1}{2}$B or $\frac{1}{4}$AB. It follows that the general formula, $(\frac{1}{2})^n$, will determine the probability of a particular combination of alleles occurring in a gamete, where n represents the number of allelic pairs. Since gametes of different allelic constitution come together to form zygotes purely by chance, the probability of obtaining a specific gametic combination in the zygote becomes $(\frac{1}{2})^n$ x $(\frac{1}{2})^n$ or $(\frac{1}{4})^n$, if each allelic pair is located on a different chromosome pair.

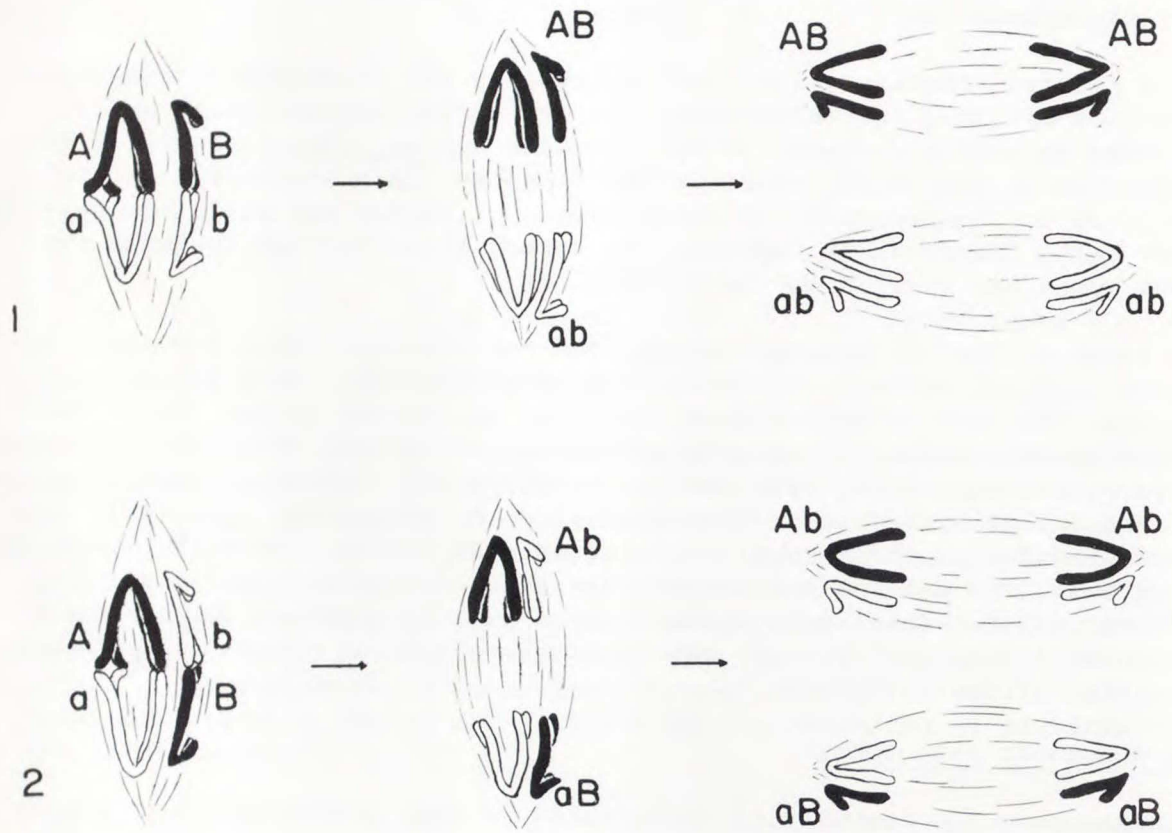

Figure 1.--Chromosome behavior at meiosis; the independent assortment of the allelic pairs, Aa and Bb, depends upon the orientation of the chromosome pairs.

The random recombination that occurs between genes located on different pairs of chromosomes is known as independent assortment. It is obvious that the larger the number of allelic pairs which control a particular combination of characters, the lower the probability of finding such a combination among the progeny of a hybrid. The search for a particular combination of desirable hereditary traits in a plant improvement program must, therefore, take into account independent assortment.

Linkage and Crossing-Over

Although chromosome numbers in different organisms vary over a wide range from as few as 2 to as many as 250 in a set, many species possess a relatively small number. For example, all species of pine show a chromosome number of 12 per set. An organism is composed of thousands of single hereditary traits; if each of these is determined by a single gene, then each chromosome must carry a considerable number of genes. It should follow, therefore, that the genes carried on a particular chromosome are transmitted together; in other words, intact blocks of hereditary characters would appear to be passed from generation to generation. The different genes located on a particular chromosome are thus said to be linked.

Breeding experiments show, however, that linkage of genes is usually not complete and that recombination of genes located on the same chromosome does occur. This phenomenon, known as "crossing-over," becomes clear when chromosome behavior during the early stages of meiosis is observed. When two chromosomes pair, each strand duplicates; as a result four strands are associated. Two of these may exchange segments so that the alleles of different genes that were previously associated are now in a new relationship, as shown in Figure 2. This exchange of segments is a regular feature of meiosis. If two genes are closely associated on a chromosome the chance of a break and exchange of segments between them is less than if two genes are far apart on the chromosome. Linkage tends to hold combinations of genes that are favorable to the organism together, while crossing-over allows greater variability than that provided by independent assortment alone. Since every plant improvement program has as its ultimate goal the development of particular combinations of hereditary characters, linkage and crossing-over must be taken into consideration in obtaining these.

Polygenic Inheritance

Our discussion has dealt only with hereditary variation that is discontinuous, i.e. where the offspring can be classified into distinct types that can be identified, at least within the limitations of dominance, as specific gene combinations. The geneticist is confronted with another type of variation, known as quantitative or continuous variation. For example, if a fast growing strain is crossed with a slow growing strain, the first-generation offspring may show an intermediate growth rate, while the F_2 progeny may show a range of types that vary from fast growers

through every type of intermediate to some that have a slow growth rate. The offspring fall into a normal distribution curve with respect to growth rate.

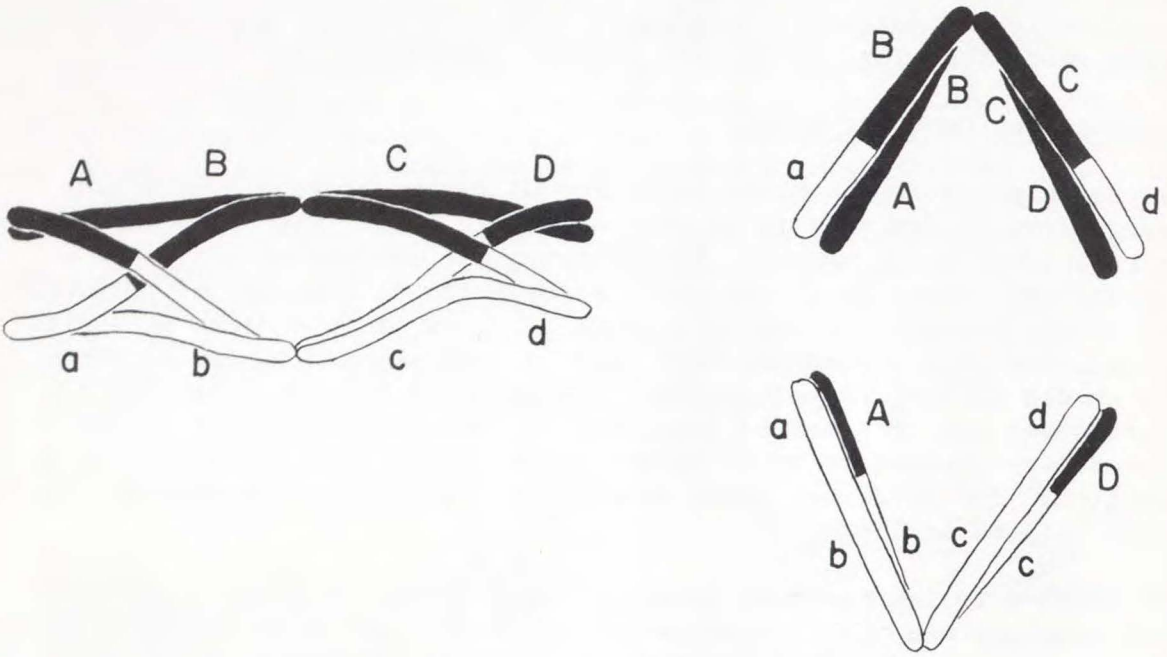

Figure 2.--Crossing-over. An exchange of segments between two of the strands results in recombination of the genes a, d with B, C, and A, D with b, c.

This pattern of inheritance can be reconciled with the concepts previously reviewed, if we make the following assumptions:

(1) The so-called quantitative characters of an organism are under the control of a number of genes, called multiple factors or polygenes.

(2) Each polygene produces a small effect which is, however, equal and additive to the effects of the other polygenes controlling a particular quantitative character.

According to this scheme, the crosses described above can be represented as follows:

Fast growth rate	X	Slow growth rate
AABBCCDDEE		aabbccddee
F_1	intermediate AaBbCcDdEe	

F_2 A range of types showing continuous variation from fast growth rate to slow growth rate. These are represented by all the combinations of alleles between the two extremes,

AABBCCDDEE ⟶ aabbccddee

This pattern of inheritance and the methods necessary for its analysis are of major importance in any plant or animal improvement program, since a great many of the hereditary traits of economic significance show continuous variation.

These are the general principles that in most organisms govern the transmission of the hereditary characteristics from one generation to the next. It is within this framework that the tree improvement specialist must work in order to obtain particular combinations of genes which possess the greatest economic value.

Group Discussion[2/]

Questions were asked concerning linkage. It was brought out that there are no known methods or techniques for determining linkage without going through the F_1 and F_2 generations. Such determination might be possible, however, where we have good knowledge of certain individual pedigrees.

Another query was "Can we make observations in natural stands for some characteristics in terms of occurrence of certain characters together?" The answer was that this might be a case of linkage, but that we also have to recognize that single genes may have multiple phenotypic effects.

2/ The report on discussion for this and succeeding articles is based on notes made by Waldemar Albertin, graduate student at the University of Michigan.

APPLICATIONS OF POPULATION GENETICS TO FOREST TREE BREEDING

by John E. Grafius[1/]

(The following is a brief synopsis of the talk Dr. Grafius presented. For those interested in further study of this problem he suggests the list of references at the end of the synopsis.)

No attempt was made to translate farm crop breeding methods to forestry. Rather, some of the more simple tools were displayed and some of the pitfalls described.

Since selection is the key to progress, one of the first questions that must be asked is, "How much of what I select for will I retain in the next generation?" Basically, this resolves itself into two parts, heritability of a trait or h^2 and the selection differential $\bar{i}$. Expressed algebraically, genetic gain $AG = h^2 \bar{i}$. The heritability of a trait was defined as the ratio of the additive genetic variance to the phenotypic variance. A simple model was used to derive the additive genetic variances, the nonadditive variance, and environmental variance. Several ways of doing this, including full-sib families and parent-progeny regressions were stressed.

The importance of genotype-environment interaction was discussed. The plant breeder must be wary of trying to select under an unstable environment.

Next it was pointed out that some so-called traits are mental constructs and not genetic entities. For example yield per acre in small grain is the product of (the number of heads per unit area) x (number of kernels per head) x (average kernel weight). Since these three things are not correlated, there is no set of genes for yield per se and one must select for the genetic traits rather than yield per acre. In other words, if there are no genes for a trait, the heritability values are spurious.

Lastly, instances of tunnel vision were cited where the breeder ended up with resistance to everything - including yield. The necessity and the feasibility of breeding for the whole organism rather than a single trait was stressed.

Selected References

Grafius, J. E. 1952. A statistical model for estimating components of genetic variance in bulk yield tests of self pollinated small grains. S. Dak. Agr. Expt. Sta. Tech. Bul. 9, 13 pp. (For a more detailed analysis of variance problems; much of the algebra is given.)

1/ Professor, Department of Farm Crops, Michigan State University, East Lansing, Mich.

_____. 1957. Biologic measurement of environment as an aid in selection. Agron. Jour. 49: 506-508. (For a discussion of genotype - environment interaction.)

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Lerner, I. M. 1950. Population genetics and animal improvement. 342 pp., New York. (For a discussion of expected genetic gain.)

Mather, K. 1949. Biometrical genetics. 158 pp., New York. (For the methods of calculating genetic variances and a clear explanation of symbols.)

Group Discussion

There was further elaboration of what the plant (tree) breeder can aim for. It was emphasized that economic and genetic traits should not be confused; that one cannot breed for something like "yield per acre." It is possible however to breed for many of the components that contribute to yield. If selecting for a certain product were the aim probably some of the values for that product could be raised but selection for individual characters would be more efficient.

It was pointed out also that some leeway should be allowed in breeding for disease resistance. Pathologists, as a rule, want types completely immune to diseases. In forest practice, however, we start with a large number of trees per acre and have a much smaller number at rotation age. Many trees, including those somewhat deficient in disease resistance, are removed in thinning. The plea was made, therefore, not to discard material, otherwise desirable, that is less than completely immune to disease attacks.

ROLE OF INTRODUCED SPECIES IN FOREST GENETICS

by Stephen H. Spurr[1/]

It has long been axiomatic in silviculture that the local or native tree is the safest and best tree to be grown by the forester. So widely accepted is this tenet that a strong naturalistic school has developed based entirely on the study of the phytosociology and ecology of native vegetation in undisturbed communities, and decrying the use of exotics for the creation of unfamiliar or artificial forest communities.

There is no question as to either the general merit of such an approach or that native vegetation is generally the safest vegetation to use in forest management. Nevertheless, the success of exotic forest trees in many parts of the world has been so great that it is desirable to examine experience with exotics if one is to arrive at a balanced view as to the importance of species origin in forest management.

Theoretically it would seem that if a given tree species has existed in a long-established free interbreeding population over a broad geographical area surrounding a given locality, natural selection should in the long run have produced local ecotypes extremely well adapted to local soil and climatic and biotic conditions. In general this seems to be the case. In the middle of the eastern white pine region, for example, there seems no question but that a local race of white pine is the best (Pauley, Spurr, and Whitmore, 1955).

The corollary seems also to be true. Wherever natural populations have not been long established, or are not freely interbreeding, or have not been distributed over a broad geographical area, then the possibility exists that natural selection has not functioned to develop a superior local ecotype, and that a population of genes from another geographical area might well be better adapted to local site conditions than the plants restricted by accident or by history to the local site. Indeed, this seems to have been the case in most instances where forest trees have proved to be successful exotics. Let us examine a few examples.

In many of the recently glaciated portions of the Northern Hemisphere, and in other relatively young geologic sites, the present forest vegetation has been present only a relatively few centuries. For example, in the State of Michigan, the southern portion of the State was exposed only subsequent to the Cary substage of the Wisconsin glaciation about 13,000 years ago, and the northern portion of the State after the retreat of the Valders ice probably 10,000-11,000 years ago. As recently as

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8,000 years ago, the vegetation of the entire State was primarily spruce. Pine became abundant in the next few thousand years, but many of the more mesophytic hardwood species became established only about 3,500 years ago, or well into historic times in terms of the Western World. There is considerable doubt whether even today heavy-seeded species such as the American beech have completed their migration north following the retreat of the ice. As a matter of fact, well documented climatic changes in recent years are certain to be reflected in the long-time distribution of tree species in Michigan (Spurr, 1956).

With so many recent changes in the distribution of forest trees, and in fact still taking place, it is not at all surprising that certain exotic species do better in parts of Michigan than the native plants. In the Ann Arbor region, the local hardwoods seem well adjusted to the local site conditions, but such important conifers as Norway spruce, Scotch pine, and European black pine do better than conifer species brought in from the nearby northern forest.

An even better example of the effect of recent geological changes in the distribution of forest types and of the success of exotics may be found in Great Britain, where revegetation following the last glaciation was slow and was composed of species that migrated north from refugia in the Mediterranean area. Most of these species were of continental origin and have proved to be poorly adapted to the maritime climate of the British Isles. Extensive trials with exotics over more than a 200-year period have convinced most British foresters that such introduced species as Sitka spruce, Douglas-fir, grand fir, European larch, and Pacific Coast lodgepole pine, are better suited to the site conditions of England than the "native" Scotch pine which reaches its best form and development in the continental climate of the Balkan region. Among the hardwoods, even the European beech which has migrated northward across England during historic times, has not yet reached an equilibrium with the present-day climate. It may be considered an exotic even though it is not known whether its introduction was or was not influenced by men living in Britain during the period of its appearance.

Actually, all of western Europe is characterized by a paucity of tree species. The geography of western Europe, with the high mountains of the Alpine region, the Mediterranean, and the deserts of North Africa, has militated against the survival of many tree species over the climatic extremes of the Pleistocene Age. As a result, most of the European forest is composed of a very few species, primarily Scotch pine, Norway spruce, two native white oaks, beech, aspen, and white birch. About as many more species were relatively uncommon but have been successfully propagated on a larger area than they occupied a century ago and may be considered exotics on most sites in western Europe even today. These include both the Austrian and Corsican strains of the European black pine, the cluster pine, and European larch. It is little wonder that, with the scarcity of species, some introduced types have a very real place in the silviculture of western Europe. These include such North American species

as eastern white pine, northern red oak, and black locust, the latter species being widely introduced in the Balkans.

The main success with exotics as tree species, however, has been in the Tropics and in the Southern Hemisphere, regions where historical, geographical, and climatic conditions have prevented a normal distribution of trees by means of natural dissemination. Many of the economic plants of the Tropics, including the coconut, beefwood, rubber tree, common teak, and mahogany, have been disseminated artificially by man and have become successful exotics in many parts of the Tropics.

In the Southern Hemisphere great success with introduced conifers has been experienced. In Australia, New Zealand, Chili, and South Africa, several million acres have been successfully afforested to Monterey pine and other hard pines. Results have been phenomenal in many cases. On the better sites, it has proved possible to raise these plantations to maturity on a 30-year rotation, with heights in excess of 100 feet achieved and yields up to 10,000 cubic feet per acre. Although Monterey pine is the most successful and most widely planted exotic, Jelecote, cluster, slash, Caribbean, and other hard pines have also been established on a large scale with good results, as has Douglas-fir. Suitable sites were available for these various species but were not accessible because of the geographical distance, as well as the interspersion of oceans and the Tropics between the native range of the species and sites in the Southern Hemisphere ecologically adapted to their needs.

A similar case may be made for various eucalyptus species in California. In the San Francisco Bay area, Tasmanian blue eucalyptus grows far more vigorously and abundantly than any of the native species on the same sites. The lack of a suitable market for this difficult-to-merchandise species in no way detracts from the fact that the species is ecologically well suited to the sites in California on which it is grown.

Although it must be admitted that many exotic plantations have failed, yet the fact remains that there have been sufficient successes to demonstrate conclusively that the local tree is not always the best tree for a given site. We may well try to extract any general principles that can be evolved from our worldwide experience with exotics.

The naturalistic school of forest site and silviculture holds, in effect, that natural selection can be depended upon to evolve a suitable species for local forest sites. In the light of present-day knowledge of genetics, we now know that natural selection must work only within the pool of genes available in a freely interbreeding population. As we realize how great the dynamic fluctuations have been in recent geologic times, and how recent have been many of the substantial changes both in the distribution of species and in the availability of sites, we now realize that in many cases a satisfactory population does not exist from which suitable natural races can be evolved. Most of the cases of successful introduction of exotics have occurred where the interposition of oceans, unfavorable

climatic zones, deserts, or simply the lack of time have prevented a suitable species from occupying an otherwise suitable site. Planting experience has shown that Douglas-fir is certainly better suited to the maritime climate and soil conditions of Scotland than the native Scotch pine. Monterey pine is obviously better adapted ecologically to growth on many of the soils of the southern temperate zone than are the species that had been able to migrate into these zones by natural dispersion channels. Certainly in the Ann Arbor, Mich., area, Norway spruce, European black pine, and Scotch pine grow more vigorously and are freer from insect and disease problems than are the native red pine brought down from 200 miles or more in the north or native shortleaf pine brought up from 200 or more miles in the south. In a real sense, the European species are more nearly native to this locale than are the exotics from other regions in the central United States.

The lesson, then, seems to be that we are not particularly concerned with whether a tree is native or exotic. It makes relatively little difference to the silviculturist whether the tree was introduced to an area by natural dissemination following retreat of the ice, by the seed being dropped from a bird flying overhead, or introduced more sanitarily as seed in an airmail envelope. What we are concerned with is that the tree must be ecologically suited to the environment in which it is to be grown. This environment includes not only the climatic and the soil factors, but also the total biotic complex of other plants, including fungi, and animals, including insects. If a tree has been grown in its geographical area for a long time, we may have learned that it is well suited ecologically to grow there and is therefore a native species. If, however, we bring in a species from outside and find by testing that it is even better suited ecologically to grow in our local community, then this species too may be considered a native and may be safely grown.

Our local species, therefore, will usually be the safest, even though they may not be the best. Many introduced species will fail, but a few may prove superior to native trees. They must, however, be thoroughly tested before they can be accepted and planted on a large scale. The aims of the forest tree improvement silviculturist, therefore, must be to put the right species on the right site. If this is done, we need not worry as to whether the tree got there "naturally" or "artificially."

As a corollary, in regions characterized by a rich and long-established tree flora, the possibilities of introducing exotics successfully are apt to be limited. Where the local flora is poor in numbers of species, however, where the trees that are present have migrated into the area in relatively recent times, and where they may not be ecologically adjusted to the local sites, then the possibilities of introducing new species into the local forests would appear particularly promising. Only by drawing upon both genetic and ecologic knowledge can the forest tree improvement specialist succeed in his mission.

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Pauley, Scott S., Spurr, Stephen H., and Whitmore, Frank W. 1955. Seed source trials of eastern white pine. Forest Sci. 1: 244-256.

Spurr, Stephen H. 1956. Michigan forests over ten thousand years. Mich. Alumnus Quart. Rev. 62: 336-341.

Group Discussion

Asked to define a "native species" as considered in his paper, the speaker did so as follows: A native plant is one ecotypically well suited to the total environment in which it grows. Accordingly 1,000 years of growth of a species in one area does not necessarily qualify that species as "native."

Also reiterated was the point that because of long-time climatic changes none of the North American hard pines appear to be as well adapted to conditions in the Ann Arbor area as are some European species. Neither red pine, whose natural range lies to the north, nor shortleaf pine, whose natural range lies to the south, is as well adapted to this locality as are some species from a greater geographic distance.

THE ECOTYPE CONCEPT AND FOREST TREE GENETICS

by Hans Nienstaedt[1/]

Introduction

Provenance, provenience, or seed source is not a well defined term. It usually signifies a seed collection made at a known location within a more or less limited population. The fame of certain proveniences such as the Riga source of Scotch pine in western Europe, German spruce (i.e. Norway spruce of German origin) in Sweden, or Sudeten larch (European larch from the Sudeten Mountains) in Denmark often has been based on practical experience gained during the last century by foresters managing the intensive forests of northern Europe. Sometimes the worth of the sources has been further established in experimental plantings in which a number of sources have been compared under relatively uniform conditions, but in most cases the statistical design has been poor. The results, therefore, were limited in scope and the conclusions rarely went beyond simply stating that certain sources were superior to others.

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Some attempts were made to delineate variational trends within the range of some of the more important species, but here again the conclusions were often sketchy and based on too few observations.

Only in the last 50 or so years have we begun to understand the distribution of the races, ecotypes, and clines within our more important timber species.

These three terms are well enough defined, but as often happens when we try to classify the multiplicity of nature, our classifications clarify some things, but muddle others. Even so the terms are useful.

1. By a race we understand a population within a species range which exhibits general similarities within itself, but varies distinctly and discontinuously from the characteristics of other populations. The variation may be qualitative as well as quantitative, but the differences between the populations are relatively minor and are not sufficient for the different populations to be distinguished as separate taxa.

2. When the distinguishing characteristics of a race are adaptive, the term is synonymous with ecotype. Distinguishing characteristics are either quantitative, qualitative, or both. Often the differences between the ecotypes show up only when they are grown together in a uniform environment. Ecotypes may show adaptation to climatic, edaphic, or perhaps biotic conditions. They may be described accordingly as climatic or edaphic ecotypes, etc. By definition variation between ecotypes is discontinuous.

3. Where the variation is gradual it is described as a cline. Clines follow geographic or climatic gradients. Although the accepted definition does not specifically state so, clinal variation is usually adaptive and often results from environmental gradients. Genetics glossaries emphasize that the variation considered in connection with the term cline is phenotypic. This connotation seems unnecessary; newer studies have shown clearly that adaptive genotypic variation also may follow geographic, climatic, or other gradients.

The majority of the commercially important tree characteristics such as vigor, resistance to spring or fall frosts, resistance to winter injury or diseases, and even straightness of stem and crown form are examples of adaptive variation and, therefore, may be ecotypic or clinal variations. In some cases - and this in part is where our concepts become muddled - they may be both. The two terms are not mutually exclusive.

We shall discuss that in more detail after first considering why adaptive variation is important in forest management and tree genetics.

The Importance of Adaptive Variation in Forest Management and Tree Genetics

The planting stock set out on a given site must be adapted to the climatic extremes in the area, or death follows. Furthermore, unless the stock is able to utilize the environment with maximum efficiency, yields will be below maximum. In spite of this, millions of trees are planted annually by individuals who know nothing about the seed source and adaptive value of the stock they plant. This is due partly to lack of interest, partly to lack of available knowledge. We need much additional information on the adaptive variation within our important species before our seed distribution policies can be fully developed.

The local seed source is generally the best grower; however, we know of cases where seed sources (ecotypes) planted outside their own environment have grown better than the native sources. Outstanding as an example is the use of German sources of Norway spruce in southern Sweden. German spruce is entirely hardy in southern Sweden, and it yields considerably more wood than the native spruce. Thus, a thorough knowledge of the adaptive variations within a species may lead to a direct increase in yields.

Some of the goals in our tree improvement programs are fast growth and disease resistance. Among the breeding methods available for their attainment are species hybridization, ecotype crossing, and selective breeding of individual plus variants. If by these methods we are to reach our goals rapidly and efficiently and get the best possible development of the different types of hybrids, we need a complete understanding of the adaptive variation within the parent species.

The majority of the species hybrids made in the past were produced in arboreta on a few specimens of doubtful origin, which probably did not represent either the best adapted ecotypes or the best biotypes of the exotic parents. In spite of this, a surprising number of promising hybrids have been made. This has been good luck. For reasonable assurance that the best species hybrids will be developed, both parents should be of seed sources adapted to the environment to be planted. In addition the hybrids should be tested under a variety of conditions to ascertain that they indeed are grown under the conditions for which they are best suited.

This does not mean that hybridization on available arboreta material is useless. Far from it; such crosses do yield valuable information on affinities within a genus and on crossability patterns, and may yield very valuable new combinations of parent traits. Very likely, however, several generations of selection in filial or backcross generations will be required for the characteristics to become established in sufficient frequencies in the progenies to make them suitable for field planting.

Stebbins (1950) has discussed a somewhat similar problem as follows: "If the adaptation of the species to its environment is of such broad general type that many different gene combinations are equally adaptive, then the chances are good that some of the segregates from interspecific hybridization will have selective value... But if certain of the adaptations possessed by the species are very exact and specific,...then the products of hybridization will almost certainly be nonadaptive."

Our growing understanding of the variation within species has made it increasingly clear that a species is a complex of ecotypes or clines in relatively delicate adjustment to a variety of environments. If the above statement is viewed on this background it can perhaps be interpreted as follows: In order for species hybridization to be successful, either the exotic parent must be of broad general adaptation or we must use a specific type of the exotic parent adapted to the environment where the hybrid is to be grown.

Another method of improvement is the crossing of ecotypes. This method also can be used to obtain increased vigor or to develop new strains combining desirable traits of two parent types. Generally speaking, the F_1 generation is intermediate between the parent types, with the segregating types manifesting themselves primarily in the F_2 generation. Here again it is clear that for the first-generation hybrids to have adaptive value suitable ecotypes must be used. Undoubtedly the F_2 generation will also have more desirable types if the parent ecotypes have been chosen with care.

Finally, one may ask how the ecotype concept affects our development of seed orchards based on individual tree selections. We cannot hope to obtain the greatest possible benefit from the seed orchards unless we restrict the distribution of seed to the limits of a particular ecotype or to a restricted portion of a cline. It goes without saying: until we have proof to the contrary, parent clones must be selected within the same areas.

It is possible that we may overcome the problem also by mixing clones from different ecotypes in the orchards thereby broadening the adaptation of the progeny. However, little or no concrete information is available and much research is needed to clarify this subject.

Methods of Studying Ecotypic Variation in Forest Trees

You are all familiar with the conventional seed source studies - field plantings of stock from many seed sources under relatively uniform environmental conditions. I will only say two things concerning them: (1) A proper statistical design is essential. No amount of care in selecting a uniform test site will substitute for the proper design. (2) In the past the accepted procedure has been to use large plots of 49, 64, 121, or more trees. Larger plots are desirable where per-acre yields

are the main objective of a test; they also give a greater number of individuals to observe and therefore a better chance of finding the rare but perhaps highly desirable variants of the populations. As an illustration, we have a planting of exotic spruces, which included 9 plots of 100 trees each of Serbian spruce. Less than 5 percent of the trees survive today, but some of them are of excellent form and reasonably good growth rate. They are perhaps potential parents of highly valuable hybrids. If we had used individual tree plots, with a total of from 60 to 100 trees, we might not have had a single tree combining hardiness, good form, and growth rate.

However, the large plots have many disadvantages and statistically speaking they are very inefficient. This has been shown by Wright and Freeland (1959). They recommend the use of 1- or 2-tree plots with as many as 100 replications depending on the degree of sensitivity desired from the tests. There is no doubt that test designs of this type will give us the answer to the majority of the problems that can be studied in an ecotype study.

Another new approach to the study of adaptive variation is early evaluation in the nursery or under controlled conditions indoors. By such tests it has been possible to evaluate form and resistance to snow damage on the basis of hypocotyl curvature as a response to a unilateral source of light (Schmidt, 1951), and relative growth rate and frost resistance in eastern hemlock (Olson, Stearns, and Nienstaedt, 1959). Ecotypic variation in seed germination responses has been demonstrated in hemlock (Stearns and Olson, 1958) and in ponderosa pine (Callaham, 1959a). Even wood characteristics such as specific gravity have been studied in nursery material and it has been demonstrated that relative values can be obtained from branchwood of seedlings (Zobel and Rhodes, 1956).

The third, least used, but oldest method of study is the taxonomic, i.e. morphological studies on samples collected on endemic trees growing throughout the distribution of a species. This method is the least effective. Because the data are based strictly on phenotypic observations and since many characteristics are highly modifiable by the environment, they cannot give an adequate basis for an evaluation of genetic variation. However, such studies undoubtedly can give much valuable information quickly and cheaply, and can help interpret the results of other experiments.

What is needed to assure the best possible evaluation of the adaptive variation within a species may be a combination of all three methods (Callaham, 1959b). Perhaps the procedure can be outlined as follows:

1. Indoor evaluation of adaptive responses and morphological traits of a large number of seed collections well distributed over the range of the species. The relative response to temperature in terms of rate of elongation and growth duration and to photoperiod

in terms of growth duration, the effects of temperature on germination, and the responses to drought conditions and low temperatures could be studied under indoor conditions. Such studies could be followed up with nursery studies over a 2- to 4-year period to help convert relative to absolute values. The plots in the nursery could be replicated single rows with bulk sowing of stock for field testing.

2. Field plantings of only a limited number of sources to make possible long-term observations of the most promising ones, to allow conversion of early development in terms of mature growth, and to let the sources be exposed to climatic extremes, which they might not experience during 4 short years in a nursery.

   Such studies could be 2-tree plots with many replications. In addition, large unreplicated plantings may be included to permit observation of many individuals for selection purposes and to be able to make observations under stand conditions.

3. Observations in endemic stands throughout the range of the species. Such observations, usually morphological and anatomical, have been of considerable value in interpreting variation patterns.

   One problem we have in interpreting the results of our field tests is the fact that they can be applied directly to a very limited environment only - ideally only in environments identical to the particular one under which the test is made. The tests must be performed under many diverse environmental conditions in different parts of the range of a species in order for us to evaluate the plasticity of a species unless we can devise methods by which we can sample growth in endemic stands and use the data in interpreting field and indoor tests. Perhaps such an approach will enable us to close the gap between actual behavior in the native habitats and the data we obtain under the artificial conditions which we ourselves create, indoors or in the field.

These then are the methods that can be used in studies of adaptive or nonadaptive variation within the species. Next, let us try to illustrate by selected examples what kinds of adaptive variation have been demonstrated, and finally let us see if we can draw some helpful general conclusions about ecotypic variation within our forest tree species.

Results of Studies of Ecotypic Variation of Forest Trees

Growth responses in terms of elongation, diameter growth, volume production, and frost hardiness are perhaps the characteristics which have been studied in greatest detail. They usually show very clear clinal patterns of variation, as for example, in eastern white pine (Pauley, Spurr, and Whitmore, 1955), Populus spp. (Pauley and Perry, 1954),

Scotch pine (Langlet, 1936, 1942-43, 1959), eastern hemlock (Olson, Stearns, and Nienstaedt, 1959; Nienstaedt, 1958) and many other species. Highly significant correlations have been demonstrated between different measures of the environmental impact and growth. Particularly the length of growing season measured in terms of frost-free period or the length of the period with a daily average of 6° C. or above has been used by many and, generally speaking, seems to be a better measure of climate than, for example, monthly average temperatures either for a single month or for a combination of two or more. Significant regression of growth responses on latitude and altitude and of growth on daylength have been found. Latitude, of course, is basically a measure of photoperiod. Altitude, and in some regions also latitude, is a measure of the variation in temperature.

Most of the relationships that have been analyzed have been straight-line relationships and have shown that if a source is moved from a short to a long growing season regime - movements from north to south or from high to low altitudes - growth is dwarfed; movements in the opposite directions lead to increased growth. Curvilinear relationships have been demonstrated in some cases (Echols, 1958), but apparently they are much less common.

If the same sources are grown and compared under different environmental regimes the relationship may or may not be the same. In hemlock, for example, the general trend among 30 seed sources was generally speaking the same on any one of 7 different constant photoperiods and under any one of 14 temperature treatments - both constant and alternating. In all cases long growing season sources grew longer than short season sources. The overall level of growth varies of course; i.e. it increases with increasing photoperiod. In hemlock, however, there is a significant difference in the slope of the curves for elongation as a function of growing season depending on photoperiod. This difference indicates that long growing season sources will show a proportionately greater increase in growth in response to a given increase in photoperiod (Olson, Stearns, and Nienstaedt, 1959). This difference in response to differences in environment is quite uniform in hemlock when a single environmental factor is changed; Langlet (1936) has shown much more complex changes in responses with changing environment and if forest trees behave like herbaceous plants, we might in some cases expect quite drastic changes in response patterns with changes in environment, as has been demonstrated for the milfoils by Clausen (1951).

The relative amount of growth is to a large extent related to duration of growth, and the duration of growth in turn is correlated to frost hardiness. It is to be expected, therefore, that frost hardiness should show the same relationships with latitude, altitude, and climate as have been described above for growth. The most complete study of ecotypic variation in frost hardiness and resistance to winter injury is probably the work by Langlet (1936) on Scotch pine. This and many other studies show that: (1) Long growing season sources have longer growth cycles

than short season sources; therefore, (2) when moved to more severe, short growing season climates they suffer from early fall frost and winter injury. On the other hand, (3) short season sources respond early in the spring in long growing season environments and are therefore apt to suffer from late spring frosts. Finally (4) the variation is gradual and therefore clinal in nature. In Langlet's study it is apparently not a straight-line relationship.

A later study by Langlet (1942-43) has shown the relationship between the growth responses mentioned and photoperiod, and other studies have also shown the dependence between photoperiod and height growth, cessation of growth, and hardiness to early fall frost. That variation in the time of bud-burst also may be an adaptation to photoperiod has been demonstrated with Douglas-fir (Irgens-Moller, 1957). His hypothesis is that higher altitudinal strains break dormancy later in the season when the danger of severe night frosts has passed, because they require a relatively longer photoperiod for bud bursting than low altitude sources.

Most studies of adaptive variation have used fairly widely scattered collections as experimental material. Localized adaptive variation in growth has also been demonstrated. One example must suffice. Squillace and Bingham (1958) have presented evidence of adaptive variation in western white pine from eight pollen sources collected on different watersheds within a 15-mile radius in northern Idaho and western Montana. The pollen was used in pollinating a number of test trees, and the general results were that pollen collected on the best site yielded the better progeny. Undoubtedly the variation is adaptive; whether it is continuous or discontinuous could not be determined from the study.

Other types of adaptive variation have been observed. Callaham (1959a) has shown very definite trends in the response of germinating ponderosa pine seed to photoperiod and temperature. Seed from areas with summer rains requires higher temperature in order to germinate, but shows very rapid germination rates when the required temperature is reached. Seed from areas with spring rains germinates at a slower rate at lower temperatures. In hemlock, southern sources require less chilling when given a favorable photoperiod than do northern sources and a higher optimal germination temperature if sufficiently chilled (Stearns and Olson, 1958; Olson, Stearns and Nienstaedt, 1959). Genetic adaptation to swamp versus upland conditions has been demonstrated in the case of northern white-cedar in Wisconsin (Habeck, 1958). Seed of upland types germinated better and showed much greater plasticity of root development than did lowland types. Adaptive variation in disease resistance also occurs. As an example, northern sources of Scotch pine show greater resistance to Lophodermium pinastri and Phacidium infestans than do southern sources. Apparent adaptive variation to Rhabdocline pseudotsugae and Phaeocryptopus Gäumanni has also been shown by Douglas-fir (Bergman, 1954).

Some characteristics which in themselves can have little adaptive value are closely correlated to growth phenomena which are. As a result they

themselves show apparent clinal variation. I am thinking of wood characteristics. Echols (1958) has shown a close curvilinear regression for tracheid length and wood density on latitude at the point of origin of seed sources of Scotch pine, and Larson (1957) found, on the basis of phenotypic observation, clinal variation in summerwood percentages in slash pine.

Finally, I would like to refer to two studies as a basis for some general conclusions regarding adaptive variation in forest trees. One is a study of lodgepole pine by Critchfield (1957), the other a study of sugar maple by Kriebel (1957). Both studies bring out a number of very important points.

1. Variation patterns within a species range are not the same for all characteristics. Thus clines of one character may be superimposed over a pattern of ecotypes or may occur within an ecotype of another character. In sugar maple, for example, injury from high insolation shows a discontinuous ecotypic variation, while variations in the time of flushing and in fall coloration form definite clines which transect the ecotypes based on sensitivity to high insolation. Moreover, within one of these high-insolation ecotypes a cline in response to insolation manifests itself. Similarly in lodgepole pine each of the principal characteristics - in this case they are morphological characteristics - is unique in its variation pattern: for example, two large areas show distinct differences in leaf width but no corresponding difference in the number of resin canals per leaf; in another large area resin canals show a distinct variation along a climatic gradient while leaf width remains essentially the same.

2. By definition ecotypes are adaptive and evolve in response to variation in environmental factors. Environmental factors vary either continuously as, for example, photoperiod with changing latitude or temperature with changing altitude, or they may vary quite discontinuously as, for example, soil types, which change abruptly with changes in the parent bedrock. It follows that adaptive variation may form clines or ecotypes depending on the variation in environmental factor from which it results.

   We still may be faced with an apparent dilemma where discontinuity in a species distribution may cause apparent discontinuities in a climatic gradient. As a result, an apparent cline within the species may be broken into distinct sections, and therefore, one might argue, distinct ecotypes. Personally, I would not favor such an interpretation unless definite discontinuous variation occurred in other traits also.

   Lodgepole pine furnishes one example of a distinct ecotype resulting from a sharply delineated environmental factor. This ecotype occurs in an area which is edaphically quite distinct from adjacent

areas occupied by the species. The population in this area is relatively homogeneous (no resin canals, narrower leaves, serotinous cones) and genetically differentiated from the rest of the species; it thus constitutes an ecotype as defined earlier in the discussion. Other characteristics, such as cone type, form interregional gradients quite typical for the cline.

3. Both studies bring into focus the problem which I mentioned in the introduction; i.e., are the terms ecotype and cline mutually exclusive? The discussion, I hope, has illustrated that they are not; it was with full justification that Stebbins (1950) used the term clinal ecotypic variation.

When we then consider that the major part of the genetic variation which determines survival value and potential yield is the result of adaptation to gradients of environmental factors and therefore is clinal or clinal ecotypic, it becomes clear that we must avoid subdividing our species into discontinuous races or ecotypes unless our conclusion is based on sufficient sampling and on observations of the responses of not one, but several characteristics under as many different environments as possible.

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Group Discussion

Most questions concerned types of variation. It was pointed out that we may have clines within ecotypes and within races. It is often difficult and hazardous, therefore, to delineate distinct races. Also we have edaphic as well as geographic ecotypes.

A comparison was made of variation in ponderosa pine and in sugar maple, both of which grow over wide geographic ranges. With the former, there is some discontinuous variation and doubtless many distinct ecotypes have developed. In the latter, variation probably is more gradual and the differences between ecotypes are less abrupt. More studies are needed, of course, to clarify variation types and patterns in both species.

Some miscellaneous discussion brought out that: (1) There are now some possibilities of obtaining tree seeds of known origin from Mainland China and North Korea. (2) Poplar cuttings cannot be imported directly from overseas. The plant quarantine organization insists on growing them in test gardens for 1 year before releasing any such cuttings. Those interested should check with their local plant quarantine office for details as to procedure.

INDIVIDUAL TREE SELECTION IN FOREST GENETICS

by Jonathan W. Wright[1/]

A selective breeding program includes both the phenotypic selection of individuals that are superior in some particular respect and the mating of those individuals in such a way as to produce superior progenies. Individual trees and their progenies are the units of study. This is in contrast to racial selection or species selection, where populations are the units of study. This distinction is important. If the job of unravelling the large differences among species and races were to be tackled on an individual-tree basis, it would never end. On the other hand, if the individual-tree records were to be discarded when studying variation within an ecotype, genetic improvement would be negligible.

In this field there are three major jobs ahead in the next few years. They are the determination of: (1) the relative amounts of individual-tree and racial variation within species, (2) the heritabilities of the most important characters, and (3) the best mating methods to achieve maximum improvement with the least effort.

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In the time available we shall be able to discuss adequately only one aspect of this subject: the genetic gains with different breeding methods. We shall consider separately those situations in which all the genetic variance is additive and when an appreciable portion of the genetic variance is nonadditive.

With Additive Genetic Variance

If it is assumed that all the genetic variance is additive, the first- and second-generation genetic gains can be calculated for most types of situations from the following formulas given by Lerner.[2/]

(1) ΔG = Genetic gain after mass selection = $\underline{i}\ \underline{h}^2$ = Selection differential x heritability (narrow sense)

(2) $\underline{i}$ = Selection differential = Mean of selected parents - mean of unselected population

(3) $\underline{h}^2$ = Heritability (narrow sense) = $\dfrac{2\ (V_m + V_f)}{V_m + V_f + V_{fm} + V_e}$

V_m, V_f, V_{fm}, and V_e = Variances due to male parent, female parent, male-female interaction, and error respectively, as derived from a 2-parent progeny test.

Formula (1) is used to estimate gain from mass selection (from selecting the best parents, growing their progeny without records as to parentage, and re-selecting among the progeny). It is also used to estimate gain from clonal selection (selecting the best parents, clonally propagating them, and selecting the best clones as parents without reference to the performance of their progeny). In the latter case the heritability is higher than in ordinary mass selection because a clonal test gives a more reliable estimate of the genetic potentiality of a tree.

The gains from family selection (selecting the best families after a progeny test) and from combined family + mass selection (selecting the best individuals within the best families) can be computed from the following formulas:

(4) $\dfrac{\Delta G_f}{\Delta G}$ = $\dfrac{\text{Genetic gain from family selection}}{\text{Genetic gain from mass selection}}$

$$= \frac{1 + (n - 1)\ r^G}{\sqrt{n\ (1 + (n - 1)\ r^P)}}$$

2/ Lerner, I. M. The genetic basis of selection. 298 pp., illus. New York. 1958.

$$(5)\quad \frac{\Delta G_c}{\Delta G} = \frac{\text{Genetic gain from family + mass selection}}{\text{Genetic gain from mass selection}}$$

$$= \sqrt{1 + \frac{(r^G - r^P)^2}{1 - r^P} \cdot \frac{n - 1}{1 + (n-1)r^P}}$$

ΔG_f = genetic gain from family selection

ΔG_c = genetic gain from combined family and mass selection

r^G = genetic correlation between individuals due to common descent

r^G = 0.5 in full-sib families

= 0.25 in half-sib families

r^P = phenotypic correlation between individuals

= $r^G h^2$ if there are no common environmental effects on members of the same family. This is true if the families are tested in 1-tree plots.

The heritability of a forest tree character is usually determined from a progeny test, in which the error variance is much lower than in a wild stand. Therefore it is necessary to multiply a "progeny test" heritability by a constant, $\underline{k}$, when calculating genetic gains based upon selection in a wild stand. This constant is defined as:

$$(6)\quad \underline{k} = \frac{\text{Heritability in a wild stand}}{\text{Heritability determined from a progeny test}}$$

In order to calculate genetic gains it is necessary to know the general breeding procedure. Several different types of forest tree breeding methods are summarized below.

TYPE I. Mass selection of open-pollinated seedlings. Collect open-pollinated seed from selected wild females, bulk the seed, establish a first-generation seed orchard, thin the orchard to the best trees after a test rotation, and harvest the seed for F_2 commercial plantings.

TYPE II. Mass selection of control pollinated seedlings. Make selected x selected matings, bulk the seed, establish an F_1 seed orchard, thin to the best trees after a test rotation, and harvest seed from the F_1 for F_2 commercial plantings.

Thinning a seed production area to the best phenotypes constitutes a variant of this method. All matings are among selected trees even though no controlled pollination is involved. However, the selection differential and therefore the genetic gain is much lower than in a planted seed orchard where each selected phenotype can be the best of hundreds of thousands.

TYPE III. Selection of half-sib families, using open-pollinated progenies. Collect open-pollinated seed from selected wild females, establish a replicated 1-parent progeny test, thin to the best families after a test rotation, and harvest seed for F_2 commercial plantings.

TYPE IIIa. Selection of individuals within half-sib open-pollinated families. Proceed as in Type III but thin the F_1 progeny test to the best individuals in the best families.

TYPE IV. Selection of half-sib control-pollinated families. Cross each selected wild female with a pollen mix containing pollen from several selected males, establish a replicated F_1 progeny test, thin the progeny test to the best families, and harvest seed for commercial production or continued experimental work.

TYPE IVa. Selection of individuals within half-sib open-pollinated families. Proceed as in Type IV but thin the F_1 progeny test to the best individuals in the best families.

TYPE V. Selection of full-sib families. Cross each selected wild female with several selected males, keep the seed separate by male and female parents, establish a replicated F_1 progeny test, thin to the best families, and harvest seed for commercial production or continued experimental work.

TYPE Va. Selection of individuals within full-sib families. Proceed as in Type V but thin the F_1 progeny test to the best individuals in the best families.

TYPE VI. Clonal selection. Establish a clonal planting with the selected wild parents, thin at the end of a rotation to the best parental-generation clones.

TYPE VII. Half-sib family selection plus clonal seed orchard. Establish a 1-parent progeny test as in Types III or IV. At the same time establish a clonal planting of the same parents. After a test rotation thin the clonal planting to the clones which were the best parents.

TYPE VIII. Full-sib family selection plus clonal seed orchard. Establish a 2-parent progeny test as in Type V. At the same time establish a clonal planting of the same parents. After a test

rotation thin the clonal planting to the two clones with the best demonstrated specific combining ability. A clonal planting thinned to the several clones with demonstrated specific combining ability belongs in Type VII rather than Type VIII. The clones will inter-pollinate among each other at random and therefore not produce the particular superior families for which they were selected.

TYPE VIIIa. Full-sib family selection plus delayed clonal seed orchard. Establish a 2-parent progeny test as in Type V. After it is evaluated, establish a planting of the two clones with the best demonstrated specific combining ability. This 2-clone planting will furnish superior seed from the time it starts to fruit until the end of the second test rotation. This is much less expensive than a Type VII seed orchard but the harvest of good seed is delayed for several years.

The genetic gains for each of these breeding methods are summarized symbolically in table 1. In the preparation of that table it is assumed that the genetic variance remains constant in the first two generations and that the number of parents is approximately the same for all breeding methods.

In seed orchards of Types II, IV, V, VI, VII, and VIII, the seed produced before the orchard is thinned is $\underline{k} \Delta G$ superior to average. This is the mass selection gain due to the phenotypic selection of the original parents in wild stands. In plantings of Types I and III the gain is only half as much because only the female parents were selected.

Any progeny test or seed orchard established with seedlings of the parental generation belongs to the F_1 generation and produces seed from which the F_2 generation will be grown. That is the reason for indicating two components for the genetic gain of all seedling seed orchards of Types I to V. The first component ($\frac{1}{2} \underline{k} \Delta G$ or $\underline{k} \Delta G$) is the gain from mass selection in the parental generation, and the second component is the family or mass selection gain in the first generation. The situation is different with clonal seed orchards of Types VI to VIII. In such orchards there can be only the one component of gain due to selection in the parental generation because the clones belong to the parental generation. Even if a clonal project were to be continued for 15 generations the clonal plantings would always be one generation behind the seedling progeny test which they were meant to supplement.

Table 1.--Summary of genetic gains with different methods of selection

Type of planting	Thinned to	Genetic mean of seed produced-- Before thinning	After thinning
MASS SELECTION METHODS. SEEDLING SEED ORCHARDS WITH NO PROGENY TESTING.			
I. Selected x OP	Best trees	$\frac{1}{2}k\Delta G$	$(\frac{1}{2}k-1)\ \Delta G$
II. Selected x selected (using pollen mix)	Best trees	$k\Delta G$	$(k+1)\ \Delta G$
FAMILY SELECTION METHODS. SEEDLING SEED ORCHARDS WITH PROGENY TESTS.			
III. Selected x OP	Best families	$\frac{1}{2}k\Delta G$	$\frac{1}{2}k\Delta G + \Delta G_{hs}$
IIIa. Selected x OP	Best trees in best families	$\frac{1}{2}k\Delta G$	$\frac{1}{2}k\Delta G + \Delta G_{c}$
IV. Selected x selected (using pollen mix)	Best families	$k\Delta G$	$k\Delta G + \Delta G_{hs}$
IVa. Selected x selected (using pollen mix)	Best trees in best families	$k\Delta G$	$k\Delta G + \Delta G_{c}$
V. Selected x selected (separate pollens)	Best families	$k\Delta G$	$k\Delta G + \Delta G_{fs}$
Va. Selected x selected (separate pollens)	Best trees in best families	$k\Delta G$	$k\Delta G + \Delta G_{c}$
CLONAL SEED ORCHARDS, WITH OR WITHOUT ACCOMPANYING PROGENY TESTS.			
VI. Selected clones	Best clones	$k\Delta G$	ΔG_{cl}
VII. Selected clones	Clones with best general combining ability	$k\Delta G$	ΔG_{hs}
VIII. Selected clones	2 clones with best specific combining ability	$k\Delta G$	ΔG_{fs}
VIIIa. Two selected clones with best specific combining ability	No thinning	ΔG_{fs}	ΔG_{fs}

Explanation of symbols used:

ΔG = gain from mass selection
ΔG_{hs} = gain from half-sib family selection
ΔG_{fs} = gain from full-sib family selection
ΔG_c = gain from combined family and mass selection
ΔG_{cl} = gain from clonal selection
OP = open-pollinated

Table 2 contains numerical estimates of the genetic mean of the seed produced by the different types of progeny tests or seed orchards after the end of the first test rotation. The values were calculated on the assumption that the "progeny-test" heritability is twice the "wild stand" heritability ($\underline{k} = \frac{1}{2}$) and that 100 seedlings of each family are grown in randomized 1-tree plots.

In this table it is noticeable that half-sib family selection is less productive than simple mass selection at heritabilities above approximately 0.25 (compare Types I and III or Types II and IV as to gain). But at low heritabilities the family selection methods--especially full-sib family plus mass selection (Type Va)--are the most productive. This is reasonable because the higher the heritability the more closely does the phenotype approach the genotype.

The genetic gains are less in seed harvested from clonal seed orchards than from the progeny tests which they accompany (compare Type IVa to VII, Type Va to VIII). This is because the clones belong to the parental generation. They are the same clones used to produce the superior families in the progeny test but there is no opportunity for practicing selection in two successive generations.

With Non-Additive Genetic Variance

If an appreciable portion of the genetic variance is non-additive it is impossible to find general solutions for relative genetic gains such as are given in table 2 because formulas 1 to 5 are applicable only to cases of additive variance. However, the symbolism presented in table 1 applies to cases of non-additive as well as of additive genetic variance.

If all the variance is additive the genetic mean of a progeny is equal to the genetic mean of the parents. This is not the case with non-additive variance because a progeny may be superior to the mean of its parents because of epistasis or dominance. Thus with non-additive variance the relative superiority of full-sib to half-sib and of half-sib to mass selection is greater than shown in table 2.

Whether the genetic variance is additive or non-additive the clones comprising a thinned Type VII orchard are the same parental clones used to produce the superior families of a Type IV seedling orchard. But if

Table 2.--Relative genetic gains from seed produced by various types of seed orchards after thinning. Calculated with formulas 4 and 5 on the assumptions that n = 100 seedlings per progeny planted in 1-tree plots, that the heritability in wild stands is half that in progeny tests ($k = \frac{1}{2}$), and that all genetic variance is additive

Type of planting		Thinned to	Genetic mean of seed produced after thinning if heritability is--				
			.10	.15	.20	.25	.30
MASS SELECTION METHODS			----------Δ G unit----------				
I.	Sel. x OP	Best trees	1.25	1.25	1.25	1.25	1.25
II.	Sel. x sel. (pollen mix)	Best trees	1.50	1.50	1.50	1.50	1.50
FAMILY SELECTION METHODS							
III.	Sel. x OP	Best families	1.63	1.44	1.30	1.25	1.14
IIIa.	Sel. x OP	Best trees in best families	1.83	1.66	1.55	1.48	1.42
IV.	Sel. x sel. (pollen mix)	Best families	1.88	1.69	1.55	1.50	1.39
IVa.	Sel. x sel. (pollen mix)	Best trees in best families	2.08	1.91	1.80	1.73	1.67
V.	Sel. x sel.	Best families	2.56	2.25	2.02	1.86	1.76
Va.	Sel. x sel.	Best trees in best families	3.08	2.37	2.12	1.97	1.88
CLONAL SEED ORCHARDS							
VI.	Sel. clones	Best clones	Not calculable. Higher than Δ G				
VII.	Sel. clones	Clones with best general combining ability	1.38	1.19	1.05	1.00	0.89
VIII.	Sel. clones	2 clones with best specific combining ability	2.06	1.75	1.52	1.36	1.26

the variance is non-additive these superior families will not give an F_2 population equal to themselves; the mean of the F_2 will regress toward the population mean. Thus a Type VII clonal orchard will give better seed than the Type IV progeny test accompanying it. Similarly a Type VIII clonal orchard will give better seed than the Type V progeny test accompanying it.

This superiority of clonal orchards over seedling progeny tests does not hold if there is a significant positive parent-progeny regression and if the seedling plantings are thinned to the best trees in the best families as in progeny tests of Types IVa and Va. In such a case the presence of a positive F_1-F_2 correlation can be inferred from the already demonstrated parent-F_1 correlation, and the F_2 seed produced by a thinned Type IVa or Type Va progeny test can be assumed to be higher in quality than can be produced by a clonal planting established at the same time.

Group Discussion

Most questions concerned the differences between eastern white pine and western white pine in susceptibility to the white pine blister rust and in the apparent differences in results of selection for blister rust resistance in the two species. Some possible reasons for the apparent greater success of selection in western white pine were given as (1) differences in testing procedures, and (2) differences in apparent severity of infection. For example, 500 cankers per tree are quite common on western white pine in the West, but are rather rare on eastern white pine in the East. The selection pressure may therefore be more intense on the western species.

SPECIES AND RACIAL HYBRIDIZATION IN FOREST GENETICS

by H. B. Kriebel[1/]

Definition of Terms

A species may be defined as a group of actually or potentially interbreeding natural populations, reproductively isolated from other such groups (Mayr, 1942). Two types of species are recognized:

1. Allopatric, occupying separate geographical or ecological areas. Examples of this type of species are Engelmann spruce and Sitka spruce.

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2. Sympatric, occupying the same or overlapping areas. Examples of this type of species are red and white spruces in northern New England.

A race is a population within a species, having general similarities and distinct from other populations, but not enough to be considered a taxonomic subdivision. An example might be Black Hills ponderosa pine.

Hybridization as a broad term refers to natural or man-made crosses of individuals of unlike genetic constitution. In discussing hybridization we are generally considering species or races. An illustration of species hybridization would be the cross of eastern white pine and western white pine. An example of racial hybridization might be a cross of New Mexico ponderosa pine and Black Hills ponderosa pine.

The Relation of Evolution to Hybridization

To understand the process of hybridization one must have some understanding of evolution. The genetic constitution of populations is constantly changing. New genes are introduced through mutation, and genotypes that survive are those best adapted to the locality. Natural hybridization plays a very important role in evolution. According to Anderson (1953) "strong evidence has been presented for the view that the most significant source of presently observed variation in many instances investigated is hybridization rather than recent mutation."

Studies of crossability patterns of particular genera, such as the one made by Duffield (1952) for the hard pines and Wright's (1955) study of the spruces, lead to hypotheses on evolution, species formation, and taxonomic relationships. This information is basic to scientific tree breeding.

Some Practical Objectives of Hybridization

(a) A tree species valuable for its timber characteristics, but lacking in resistance to a potent disease or insect pest, may be combined with a closely related resistant species to produce a hybrid including all the desirable characteristics. The well-known hybrid of European and Japanese larch, for instance, shows resistance to the larch canker to which its European parent is highly susceptible. The hybrid between European Populus tremula x North American P. tremuloides shows resistance to rust and aspen scab.

(b) A species desirable for a certain region from a forestry standpoint but lacking in winter or summer hardiness may be combined with a hardy species to produce a hybrid adaptable to the region. For example, Piatnitsky (1954) reported a drought-resistant hybrid, Caucasian oak x English oak. The hybrid has 30 to 40 percent less water loss in transpiration than English oak. A cross of pitch x loblolly pine is noticeably less susceptible to low

temperature injury in southern Illinois than is loblolly pine, has reasonably good form, and may have possibilities north of the area to which loblolly itself can be extended (Lorenz and Spaeth, 1953). This hybrid is also being used extensively in South Korea where the climate is too cold for loblolly pine (Hyun, 1956).

(c) Two related but geographically or ecologically isolated species may, when crossed, yield a progeny showing hybrid vigor (i.e., greater vigor than either of the parent species when grown in the same locality). A number of hybrids of European and North American poplars and aspens show this characteristic of heterosis or hybrid vigor (Schreiner, 1959). Another illustration is the hybrid western white pine x eastern white pine.

Two Methods for Production of Hybrid Seed in Commercially Usable Quantities

(a) Direct utilization of F_1 or first-generation hybrid seed produced by hand-controlled pollination is possible if viable seed yields are fairly high, or by open pollination if trees are isolated from others of the same species.

(b) Alternatively, the F_1 generation may be utilized as an intermediate for the production of F_2 generation hybrids in seed orchards by open pollination or by controlled pollination, often through a backcross with one of the parent species.

The Korean program of mass production of hybrids of the pitch x loblolly cross is an illustration of the direct utilization of the F_1 hybrid. In 1956 over 23,000 pollinations were made. It is estimated that the cost of the trees is only about one-third more than that of regular Scotch pine transplants (Hyun, 1956). Another example is the widespread outplanting of the Dunkeld larch.

Although the F_1 generation hybrids are fairly uniform, the F_2 generation yields a wide range of genotypes and phenotypes. If we take a hypothetical example of simple dominance such as that presented by Langner (1952) in which three phenotypic characters are under study, the F_2 generation will segregate into 27 genotypes. Only one out of 64 trees will be homozygous for all three desirable characters. On the other hand, there will only be 8 phenotypes, and 27 out of 64 trees or 42 percent will have the combination of all three desirable phenotypic characteristics. For a forest plantation in which thinnings are to be made, this is ample. This practical type of approach is being used at the Western Institute of Forest Genetics at Placerville where a seed orchard of lodgepole-jack pine hybrids has been producing low-cost F_2 hybrid seed for several years; the seedlings look promising as a rapid pulpwood producer (Duffield, 1954).

Second-generation hybrids may be produced by backcrossing, that is, crossing a hybrid to one of its parental types. This technique is useful in transferring single characters such as insect resistance to non-resistant but valuable stock. For example, the Jeffrey pine x (Jeffrey pine x Coulter pine) backcross combines the weevil resistance of Coulter pine with the desirable wood quality, form, and vigor of Jeffrey pine (Libby, 1958).

Second-generation crossing may involve a third species. One use is to bridge an incompatibility between two species. Holst (1957) is using this method in spruce breeding. Norway spruce is a desirable species for eastern Canada, but is not resistant to the white pine weevil, as is white spruce. Crosses between Norway and white spruces have not been successful. However, by crossing Norway spruce with another species such as Sitka spruce, and later crossing the hybrid with white spruce, it is hoped that a superior resistant type may be obtained. Another use is to introduce new genes to improve an existent hybrid. This has been done in chestnut breeding. The Japanese chestnut x American chestnut hybrid has fairly good form, but its Japanese parent is only partially blight resistant. The high degree of blight resistance of the Chinese chestnut can be combined by crossing it with this hybrid. Second-generation Chinese x (Japanese x American) hybrids in Connecticut look very promising, attaining 40 feet in height at 16 years with good form and a high degree of blight resistance (Nienstaedt and Graves, 1955).

Influence of Biology and Economics on the Selection of Breeding Material

It is important to know the biological and economic characteristics of the species in the genus, such as site adaptability. Black and red spruces, for example, differ in relative toleration of wet or dry sites. Branch habit and tree form may vary greatly from one species to another, as in the case of Japanese red pine versus Japanese black pine. There may be wide variation in disease resistance, pulping qualities, and other characters.

The degree of gain possible by using species hybridization in addition to race and individual selection depends upon the particular characters for which selection is being made. Such characters as fiber length and specific gravity show considerable intraspecific, in fact individual, variability among the southern pines. In this case improvement is possible by selection, propagation, and the establishment of seed orchards. Again, in sugar maple wide variability in sugar content of the sap is indicated, whereas no other species of maple approaches Acer saccharum in this respect. Here again breeding of individual selections rather than species crossing is the best approach. On the other hand, in eastern white pine there is a relatively slight variability in genetic capacity to resist white pine weevil attack. If any improvement is made it will probably be through hybridization with a more resistant species, possibly Balkan pine.

Interracial crosses may be useful when individual variability within a region is only moderate but pronounced regional differences exist. If a sufficient period of gene isolation has elapsed, hybrid vigor may be obtained. Helge Johnsson (1956) reported heterosis in European aspen crosses using parents from different latitudes. He advocated seed orchards constructed of clones from rather large areas, making it possible to use the seed from the orchard over a wide area. The positive effects of heterosis counterbalance any negative effects of moving provenances. Nilsson (1958) reported very vigorous crosses of Swedish and continental Norway spruce. These interracial hybrids are superior to Swedish spruce in growth, and superior or equal in growth to continental spruce and more resistant to frosts. According to Wettstein (1958), investigations of characteristics of individual races of Scotch pine show the possibility of selective genotype breeding for certain desired characteristics such as form of tree, rate of growth, resistance to disease and cold, shade tolerance, and weight of seed.

Influence of Geographic Origin of Parents and of Planting Location of Progeny on Hybrid Performance

The seed source of parent trees may vitally affect hybrid performance. An excellent illustration at Placerville is the relatively slow growth of the hybrid western white pine of California origin x Himalayan pine in comparison with the immediately adjacent hybrid western white pine of Washington origin x Himalayan pine (Duffield and Snyder, 1958). Of the numerous crosses between European aspen and quaking aspen made in Denmark, the most promising so far seems to be the hybrid between European aspen from Poland and quaking aspen from the district around Vancouver, British Columbia, raised with material from populations cultivated in Denmark (Larsen, 1956).

Consideration must also be given to the region in which the hybrid will be used. In the case of the hybrid western white pine x eastern white pine, plantations in the Western States show hybrid vigor, but less satisfactory results have been obtained in Wisconsin. Langner (1951) states that "the highest growth capacity of hybrids can be expected when pure species from spatially isolated, climatically similar regions are crossed with one another and the hybrids are grown in this same sort of climate. If one of these requirements is not met, the effect of limiting factors is expressed, whereby growth of the hybrid is held down to a level lower than that of the parents."

Individual selection and tree breeding must go together. Obviously although a particular species cross may have hybrid vigor or disease resistance, if one of the parents is badly forked the loss may outweigh the gain. Likewise carefully selected specimens may be expected to produce better hybrid progeny than run-of-the-mill trees. Certain types of selection are unavoidable, such as selection for fruitfulness. Sex of the tree may be important; in dioecious species such as poplars, reciprocal crossing would obviously be impossible unless both male and female trees were available.

Inbreeding

Inbreeding consists of crossing a tree with itself or another individual of identical genetic constitution if it is clonal material. There is great variability in self-fertility of forest trees. Among the maples, some seem to be self-fertile and some self-sterile (Piatnitsky, 1934).

Pines are quite variable. Self-sterility is high in Japanese red pine and low in Japanese black pine, for example (Toyama, 1950). The degree of self-fertility may also be quite variable among individuals of a single tree species, as is the case in Douglas-fir (Orr-Ewing, 1954).

Inbreeding depression is common in many species; western white pine seedlings provide an excellent illustration of this effect (Bingham and Squillace, 1955). Juvenile depression in some character such as height growth may not necessarily follow inbreeding, however. The writer has found no clear evidence of such an effect in sugar maple. In general, the closer the character is related to fitness, the more it is subject to inbreeding depression (Lerner, 1958).

Inbreeding may be used for later outcrossing. In England, both European and Japanese larches are being inbred for later species crossing, with the expectation of obtaining a pronounced heterotic effect in the hybrids (Matthews, 1955).

Obviously, a knowledge of degree of self-sterility is important in controlled pollination work and establishment of seed orchards. The possibility of selective fertilization also needs to be explored. A tree may be self-fertile when artificially pollinated, but under natural crossing its own pollen may be discriminated against in favor of pollen from other trees (Squillace and Bingham, 1958).

Breeding Technique

Breeding technique includes at the outset collection, extraction, and storage of pollen. Flowers may be collected from trees in the field, picked catkins, branches forced indoors, or even branches grafted in the greenhouse. In some cases, as in poplars and elms, the seed can be produced on cut branches.

Pollen extraction techniques range from flat sheets of paper to the elaborate extractors developed at Placerville (Cumming and Righter, 1948). One simple type is a sleeve of sausage casing. Another is a small airtight box with removable screen gauze and stopper funnel at the bottom.

Pollen storage techniques vary with the species. Pine pollen can be stored at 25- to 50-percent relative humidity at 38 to 40 degrees F. (Duffield, 1953). Deep-freeze techniques may prove more satisfactory for long-term pollen storage. Year-old pollen often gives high seed

yields but a low percentage of viable seeds (Wright, 1959). However, at times it is necessary to use year-old pollen, as in pollination of pines in Ohio with pollen from western soft pines (limber, sugar, western white, and whitebark pines) on which pollen is late in maturing.

Flowers are isolated by bagging to prevent random open pollination. Observation of the rate of development of flowers is of the utmost importance to the success of controlled pollination. Pollen must be applied at the time the flowers are open and receptive, although our present knowledge of duration of period of receptivity is quite limited for many species. While much valuable data lie buried in tree breeders' notebooks, relatively little has been published. Detailed information of this type has only recently been published on Scotch pine (Ehrenberg and Simak, 1957), although this is one of the world's most intensively studied tree species.

The method of pollen application will depend on the mode of pollen transport. Pollen can be brushed on with a small brush or with the male flowers themselves in the case of an insect-pollinated species. If the species is wind-pollinated, pollen is usually blown into the bag by means of a rubber bulb and hypodermic needle. After the pollination period is over, the bag is generally removed, although it may be kept on, or another bag put on, for protection against insects.

Careful labelling and recordkeeping are essential. A soft aluminum tag with paper backing and copper wire is useful; it can be numbered in advance and placed in the bag with a wad of non-absorbent cotton to be wrapped around the shoot at the mouth of the bag. A cloth streamer is often attached to improve visibility. Records are kept of every pollination; a simple type of record sheet adaptable to a pocket notebook is illustrated in U.S. Dept. Agr. Cir. 792, by Cumming and Righter (1948).

Seed collection and seed handling are time-consuming operations because of the meticulous care required to retain the separate identity of each seed lot.

Evaluation of Hybridity

Identification of hybrids, both natural and artificial, consists of grading the putative hybrids for physical characteristics of seeds, cones, twigs, and leaves; study may include the internal anatomy of the leaves; also their color, pubescence and number and position of stomata. Points of interest are not only taxonomic characters but also such characters as resin chemistry in pines (Mirov, 1942, 1946).

Size measurements may be taken of leaves and buds, and analyses made of the number and degree of appression of bud scales. Comparisons may be made with parental physiological responses such as growth phenology, winter hardiness, and drought resistance.

The number of characters requiring scoring in a hybrid index depends on the reliability of the individual characters, and may range from one to several dozen. Zobel (1951) used 12 characters for evaluating natural hybridization between Coulter and Jeffrey pines, including cone, seed, foliage and oleoresin characters. In other work with pines, effective discrimination of F_1 and F_2 hybrids of knobcone and Monterey pines is possible using seven characters (Bannister, 1958). Recently, Schütt and Hattemer (1959) reported that analysis of pine hybrids solely by means of the characters seen in transverse needle sections is insufficient. Mergen (1959) has recently reported on studies indicating that stomate distribution is a reliable criterion of pine hybridity.

Polyploidy

Nilsson-Ehle's discovery of the vigorous triploid aspen in 1935 (Nilsson-Ehle, 1936) aroused interest in the use of polyploids in tree breeding. The triploids were 11 percent taller, 10 percent larger in diameter, and 36 percent higher in volume than adjacent diploid aspens of the same age. Triploids are generally sterile, but occasionally crosses of diploids and triploids yield tetraploids, permitting quantity production of triploids.

Examples of polyploids are the natural triploid of European white birch (Johnsson, 1944), natural tetraploids of Norway spruce in Sweden (Kiellander, 1950), tetraploid European larch, and tetraploid Caucasian alder (Larsen, 1956).

Polyploids can be used in hybridization. The diploid Italian alder x tetraploid Caucasian alder has vastly greater growth than open-pollinated Italian alder. Extraordinary vigor was shown by a triploid hybrid from a controlled pollination of European larch with western larch. Natural polyploid hybrids have been discovered, as in the case of the natural triploid hybrid of Betula pubescens and Betula pendula, discovered by Helms and Jorgensen (Larsen, 1956).

Conclusions

1. Hybridization of species and races is a natural process of evolution that is continually occurring in forest trees as a result of climatic changes and other factors promoting changes in gene distribution.

2. Heterosis or hybrid vigor is fairly common among tree crosses of species from climatically similar but geographically isolated regions, and has its greatest expression when hybrids are planted in climatic regions similar to those of the parents. If climates of the parent species are different, race research is particularly important to make the best crosses for use in particular regions.

3. Inherent tendency to withstand or succumb to diseases and insect pests not infrequently is common to an entire species or race, by virtue of long-term previous exposure to or isolation from these injurious agencies.

4. Species or racial hybridization may be the most effective technique for tree improvement in such cases, by the combining of genes for resistance with genes for other desirable characters.

5. Hybridization is most effectively used in connection with selection - not only race selection, but careful selection of superior individual specimens from each of the parent species.

6. Finally, hybridization is already beginning to be used for mass production of superior tree types both in this country and abroad. There is every reason to believe that it will play an increasing part in scientific forest management.

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MINERAL NUTRITION OF PLANTS

by A. G. Norman[1/]

Interest in the problem of the mineral nutrition of plants depends on the point of view of individual workers. Agronomists may be concerned with plant nutrients as they affect mineral composition and plant products in relation to utilization as food or feed, or they may be concerned with the capability of the soil to supply needed nutrients and the correction of deficiencies and inadequacies by fertilizer application. Those working with forest crops presumably care not at all about the mineral composition of the product, but may be concerned with site differences explicable in terms of available nutrients or nutrient inadequacies limiting growth rate.

There are certain genetic characters in crop plants that affect the composition of the plant, but the immediate ionic environment of the root may becloud the genetic-controlled composition differences. In forest genetics there has presumably yet been little opportunity to study characteristics that might affect nutrient utilization and composition, except insofar as these might be correlated in some way with growth rate.

It is important to say at the outset that most basic studies on the mineral nutrition of plants are carried out on young, quick-growing annuals. Mature woody species are less frequently studied.

It is now generally conceded that the search for plant nutrients is no longer a rewarding field of study, and there is general agreement on a list of twelve elements, six of which are usually regarded as major nutrient elements on the basis of the amount required, and six minor elements, no less essential but needed in small amounts. The proof of essentiality of major elements is easy but becomes more difficult with minor elements. Here the criteria of essentiality becomes important. It is necessary to show that the plant fails to complete its normal vegetative and reproductive sequence in the absence of an element believed essential, that the element in question cannot be completely replaced by another, and that the test plant species is fully representative. These criteria cannot be said to be fully met with many forest trees.

1/ Director, University of Michigan Botanical Gardens, Ann Arbor, Mich.

Soil-grown plants contain many elements not shown to be essential in solution culture studies. Soil-grown plants always contain appreciable amounts of aluminum and silicon. Is the aluminum- or silicon-free plant a normal plant?

Complete explanations as to why certain elements are essential cannot be given. Paradoxically, more progress has been made in recent years in accounting for the minor elements. Enzyme systems known to be present in plant cells specifically require certain metals for activation. Deficiencies or inadequacies in supply are, therefore, accompanied by bio-chemical inadequacies in some or all of the cells of the plant; these bio-chemical inadequacies result in repression of growth and morphological abnormalities that are regarded as symptoms, and are recognized and described but not explained. Perhaps, of all elements, potassium presents the biggest enigma. In the ash of many trees potassium may be the largest single component. Potassium is an element of great mobility, and it may be that its role is to maintain an optimum ionic environment within the active cells for such components as the mitochondria and microsomes.

It has long been the goal of plant physiologists to be able to express the quantitative requirements of plants for mineral nutrients in order to be in a position to define an adequate diet. This is most difficult because the amount of a nutrient taken up is the function of supply rather than demand, and may also be affected by the water regime. Luxury consumption, that is uptake beyond the level accompanied by increased growth, is a familiar phenomenon. The requirements of plants for nutrients are not constant through their whole period of growth. Making available at one time all the nutrients in kind and amount that would be required for maximum growth would not necessarily ensure the optimum development of the plant. Initially it would be solidly in the luxury consumption zone, but some of the elements accumulated are not readily mobile within the plant and cannot later be transferred from older tissues to new tissues.

Although higher plants can be grown to maturity in culture solutions, the soil constitutes the normal root environment. In soil the quantity of nutrient and other elements actually in solution at any one time is very small. The crux of the situation is that the rate of renewal or replenishment may determine the quality of a soil. Exchange reactions between the clay colloids, the soil solution, and internal and external root surfaces are of great significance in cation uptake.

The actual mechanism of nutrient uptake has turned out to be a more troublesome problem than was earlier supposed, but the availability of radioisotopes has been particularly helpful. There has been revision of the classical concept of the root and acceptance of the view that an external solution can freely penetrate some parts of the root tissue spoken of as "apparent free space." The energy-requiring process of accumulation from the free space is partially selective and can be halted

by respiratory inhibitors. The essential features in uptake may be the binding of the nutrient ion to a carrier, the carrier being a compound, perhaps analogous to an enzyme. Carriers are presumed to possess specificity for particular ions, but this specificity is not absolute. Other ions chemically related may also be bound. The carrier-ion complex is presumed to be able to pass through some form of barrier or membrane not permeable to the ion alone. The evidence for the existence of ion carriers is indirect but is supported by kinetic studies.

Not all workers are in agreement with this picture of uptake mechanisms, but this new concept does permit explanations to be given for some of the puzzling features of plant nutrition, such as the presence in plants of substantial amounts of nonessential elements, certain aspects of luxury consumption, the inability to determine the quantitative requirements, the ready entry of large organic molecules into roots, and the leakage of inorganic and organic solutes from roots. There is a strong probability that, within the next few years as this concept matures and is subject to rigorous testing, there will be developed a more satisfactory account of the complicated steps involved in the nutrition of plants, both annual and perennial.

CURRENT FOREST TREE IMPROVEMENT RESEARCH IN THE LAKE STATES

by Paul O. Rudolf[1/]

Some 70 research workers in 11 research agencies presently are conducting 113 formal forest tree improvement studies in the Lake States, according to a survey made by the Lake States Forest Tree Improvement Committee in 1959. In addition, most of these agencies are also carrying on a number of less intensive informal studies. Many of these research agencies are cooperating with each other in this work, but 56 other, mostly non-research, agencies have also aided the projects through providing land, field help, financial assistance, nursery facilities, seed, and other items.

Current tree improvement studies in the Lake States concern more than 15 genera, but almost three-quarters of them involve the pines, spruces, and poplars. Red pine is receiving greatest attention in its genus and is followed in order by jack pine, eastern white pine, and several exotic species. In Picea, white spruce is most prominent, followed by black

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1/ Chairman, Research Evaluation, Coordination, and Planning Subcommittee of the Lake States Forest Tree Improvement Committee, and Research Forester, Lake States Forest Experiment Station.

spruce, Norway spruce, and several exotic spruces. The native quaking and bigtooth aspens are the major Populus species being studied in this region, but a number of other species and hybrids also are involved.

Current projects have been classified into 33 subject-matter categories. About half of the studies concerned variation, both natural and induced. Racial variation was the most common category; it included more than one-fourth of all studies. Most of the other studies are in the fields of supporting sciences, mostly in botany (especially plant physiology) and special techniques (notably vegetative propagation). Fundamental genetics research accounts for about 5 percent of all current studies.

Brief reports on current research were presented at the conference by representatives of the research agencies, as follows:

Forest industries - J. W. Macon
Institute of Paper Chemistry - D. W. Einspahr
Quetico-Superior Wilderness Research - C. E. Ahlgren
Forest Products Laboratory - M. Y. Pillow
University of Michigan - S. H. Spurr
Michigan State University - J. W. Wright
University of Minnesota - Paul O. Rudolf (for Scott S. Pauley)
University of Wisconsin - R. R. Hartig and R. F. Patton
Lake States Forest Experiment Station - Paul O. Rudolf

With one exception these reports are not included in the proceedings because they are covered in a separate publication.[2/] The report for forest industries is appended because it includes considerable information not available elsewhere.

These surveys give a reasonably good account of present forest tree improvement research in the Lake States. Of course, any quantitative listing of projects overlooks differences in size, cost, value, and quality, but this one does help to show where current interests and activities are greatest. It also helps point out areas where more emphasis may be needed. So not only do we know better where we are, but also we have a clearer view of the way we should go.

2/ "Forest Tree Improvement Research in the Lake States: A Survey by the Lake States Forest Tree Improvement Committee," Lake States Forest Experiment Station, Station Paper 74, September 1959. Copies of this report can be obtained by writing to the Station at St. Paul 1, Minn.

INDUSTRY'S PART IN FOREST TREE IMPROVEMENT RESEARCH IN THE LAKE STATES

by J. W. Macon[1/]

Forest tree improvement research in the Lake States so far has concentrated on basic or quasi-basic problems in an effort to accumulate a store of knowledge that may eventually be adapted to practical forest management. Because of the nature of the general program, the momentum of this work has been set by public and educational research organizations. But many of the projects could not have been developed to their present state of accomplishment without the cooperation of the Lake States forest industries.

Relatively little original work has been done by individual forest industries. Only two companies have projects that date back more than 2 or 3 years. However, industry has an important role in tree improvement research through its cooperative efforts with Lake States research institutions. Also through this cooperative work, industrial foresters have been exposed to the tree improvement science and scientists, and their curiosity has been aroused to the point where a number of them are beginning a few experiments of their own. Much of this work may be haphazard, but it does contribute to the background that industry will need before it can apply some of the products of forest tree improvement research.

Cooperation by industry in tree improvement research work has been in three general categories. The first of these consists of grants of money to support research. The Institute of Paper Chemistry's genetics program, which is supported by paper companies, is an example of this type of cooperation.

A second form of cooperative work involves the release of land or other facilities for use by the research institution. The work of the University of Minnesota in the D. M. Gunn Memorial Park illustrates this type of collaboration. The third form of cooperation consists of actually sharing the work. Some of the Lake States Forest Experiment Station's seed source studies are specimens of this kind of cooperation.

In actual application of tree improvement knowledge, industry has taken the lead in one field - the growing of forest planting stock from seed of presumably better-than-average genetic quality. The seven industrial forest nurseries in the Lake States produce about 7 million trees annually. All of these nurseries have a seed-quality program wherein at least

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1/ Forester, Consolidated Water Power and Paper Company. Mr. Macon represents the Lake States Council of Industrial Foresters on the Tree Improvement Committee.

part of their seed requirements are collected under direct company supervision from selected trees and stands.

Based on a September 1959 survey of members of the Lake States Council of Industrial Foresters, the following companies are engaged in some form of tree improvement research work:

Blandin Paper Company.--Through the Blandin Foundation the Blandin Paper Company has given money to the University of Minnesota to finance tree improvement work.

The University has established a Tree Improvement Arboretum on company land in the D. M. Gunn Memorial Park. Selected Populus and conifer trees and hybrids are planted here.

The company cooperated with the University in the establishment of a white spruce seed source planting in 1958.

It also collects as much seed as possible from selected trees or stands for its nursery.

Consolidated Water Power and Paper Co.--In 1950, 1951, and 1956 the company established plantings of white spruce transplants selected in the nursery for exceptionally fast height growth. The 1956 planting contains the tallest 700 transplants produced in the nursery that year. Control trees are included in the plantings.

They supervise the collection from selected trees or stands of most of the spruce seed used in the company nursery.

Diamond Match Division - Diamond-Gardner Corporation.--The company cooperates with the University of Minnesota on field testing aspen and paper birch hybrids and in studies of grafting superior aspen scions on natural aspen suckers in the field.

Owens-Illinois.--The company has experimented with gibberellic acid applications to aspen, red pine, and white spruce.

Kimberly-Clark Corporation.--The corporation helps support the genetics section of the Institute of Paper Chemistry.

They cooperate (1) with the Institute in the field testing of aspen diploids and triploids, (2) with the University of Wisconsin and Dow Chemical Company on hybrid aspen field testing, and (3) with the University of Minnesota on developing techniques for establishing seed orchards.

They supervise collection of seed for the company nursery from selected trees and stands. Seed lots are labelled and the stock is planted in the vicinity of the geographic origin of the seed.

Marathon.--This company supports the genetics section of the Institute of Paper Chemistry, and cooperates with the Institute in field testing aspen polyploids.

Minnesota and Ontario Paper Co.--They are developing techniques for the establishment of red pine, white pine, jack pine, white spruce, black spruce, and balsam fir seed orchards.

Mosinee Paper Mills Co.--This company is cooperating with the Lake States Forest Experiment Station in its study on racial variations of jack pine.

Nekoosa-Edwards Paper Co.--The company has established seed source studies of jack pine, red pine, black spruce, and white spruce from 1954 through 1958.

They are cooperating with the Lake States Forest Experiment Station on jack pine seed source studies.

They supervise the collection from selected trees and stands of much of the seed used in the company nursery.

Northwest Paper Co.--They supervise collection of much of the seed for the company nursery from selected trees and stands.

Rhinelander Paper Co.--This company supports the genetics section of the Institute of Paper Chemistry and cooperates with the Institute in field planting polyploid aspen and larch.

They cooperate with the University of Wisconsin on white pine blister rust resistance tests.

They supervise collection of much of the seed for the company nursery from selected trees and stands.

ACTIVITIES OF THE LAKE STATES FOREST TREE IMPROVEMENT COMMITTEE

by Paul O. Rudolf[1/]

Subcommittees

An important part of the Lake States Forest Tree Improvement Committee's work in encouraging and coordinating forest tree improvement activities in the region is done by a series of subcommittees, three of which are active now. Their accomplishments can be reported briefly as follows:

1. The Subcommittee on Registering and Marking Selections in the Lake States has prepared and distributed a report[2/] which includes a list of registers of superior trees and stands in the region, directions for establishing a regional register of unique or unusual trees, and recommendations for marking and registering selections in the field. The subcommittee consisted of H. E. Ochsner, Chairman, Earl Adams, Scott S. Pauley, A. J. Riker, and Jonathan W. Wright. With the publication of its report the subcommittee has been discharged.

2. The Subcommittee on Research Evaluation, Coordination, and Planning also has prepared a report[3/] which has received initial distribution at this conference. This report contains brief summaries of all active, formal forest tree improvement projects in the Lake States. It also includes a classification of projects by species and subject-matter categories, a list of research workers, and a list of cooperators. The subcommittee consists of Paul O. Rudolf, Chairman, R. A. Brink, H. L. Mitchell, Scott S. Pauley, and Stephen H. Spurr. It is a continuing subcommittee.

1/ Executive Secretary, Lake States Forest Tree Improvement Committee.

2/ Copies were sent to all those on the Committee mailing list. Additional copies can be obtained from the Executive Secretary.

3/ Copies can be obtained by requesting Station Paper No. 74, from the Lake States Forest Experiment Station, St. Paul Campus, St. Paul 1, Minn.

3. The Subcommittee on Forest Tree Seed Certification presented a report at this conference. It summarizes present forest tree seed certification activities in the United States and recommends that a set of certification standards be developed suitable for use in the Lake States. Copies of the report will be sent to all those on the Committee mailing list. This subcommittee, which is still active, consists of J. W. Macon, Chairman, W. H. Brener, R. A. Brink, F. J. Hodge, A. C. Hodson, and P. O. Rudolf. (Since October 1959 W. H. Brener has been chairman.)

Committee Affairs

Members of the Lake States Forest Tree Improvement Committee serve 4-year terms. At each biennial conference, terms of half the members are completed and an equal number of new appointments or reappointments are made. At that time new officers also are elected. At the close of the Ann Arbor conference, therefore, Committee membership and officers were as follows:

Name	Representing	Appointment expires
Stephen H. Spurr (Chairman)	University of Michigan	1961
John Macon (Vice-Chairman)	Lake States Council of Industrial Foresters	1961
Paul O. Rudolf (Executive Secretary)	Lake States Forest Experiment Station	1961
Earl J. Adams	Minnesota Conservation Department	1961
W. H. Brener	Wisconsin Conservation Department	1961
R. A. Brink	University of Wisconsin	1961
D. W. French	Central International Conference on Forest Insects and Diseases (Pathology)	1963
F. J. Hodge	Michigan Conservation Department	1963
P. N. Joranson	Institute of Paper Chemistry	1963
E. N. Lee	North Central Region, U. S. Forest Service	1963

Name	Representing	Appointment expires
H. L. Mitchell	Forest Products Laboratory	1963
Scott S. Pauley	University of Minnesota	1963
Donald W. Renlund	Central International Conference on Forest Insects and Diseases (Entomology)	1963
Jonathan W. Wright	Michigan State University	1961

The next biennial tree improvement conference in the Lake States will take place in 1961. In the normal order of rotation, it should be held in Wisconsin. The group agreed, therefore, to accept the invitation of Director M. B. Dickerman of the Lake States Forest Experiment Station to hold the next conference at the Northern Institute of Forest Genetics near Rhinelander, Wis. By 1961 facilities now under construction and development at the Institute will be ready for use and inspection. Furthermore, interesting field trips can be arranged in the general vicinity to cover tree improvement work of several agencies. John Macon, Vice-Chairman of the Committee, will be in charge of arrangements for the 1961 conference.

Resolutions

A committee of R. F. Patton (Chairman) and J. W. Macon prepared the following resolutions which were adopted unanimously by the Conference:

"It is resolved that members of the Fourth Lake States Forest Tree Improvement Conference unanimously express a vote of thanks and appreciation to the following:

"Dean Stanley G. Fontanna of the School of Natural Resources for his cooperation and financial support in making arrangements for the meeting.

"The University of Michigan Extension Service for their help in the details of planning and registration.

"The local committee (S. H. Spurr, J. W. Wright, and F. J. Hodge) who managed all local arrangements and planned the fine program.

"Professor A. G. Norman for his willingness on short notice to substitute for Scott Pauley as the banquet speaker and for his able summation of some of the present thinking on nutrient uptake by plants.

"The speakers who so graciously took of their time in taking part in the 'Short Course in Forest Genetics.'

"The Officers of our Forest Tree Improvement Committee who have guided the activities of the group during the past 2 years.

"Also to Scott Pauley is sent regrets of the group that he could not attend the meeting. His presence was missed by all."

The Executive Secretary has expressed the appreciation of the Conference and the Lake States Forest Tree Improvement Committee to all those named in the resolutions.

FIELD TRIP HIGHLIGHTS

On October 7 conference members participated in a field trip.[1/] Visited were the Michigan Conservation Department's new Southern Michigan Nursery and three of the University of Michigan's demonstration and research forests.

Southern Michigan Nursery.--The newly-developed nursery in southern Michigan is one of four operated by the Conservation Department. Its major advantages are that (1) it will permit lifting nursery stock early enough in the spring so that farmers can do their tree planting before the press of the regular farm work commences, and (2) it will make it possible to produce some of the species of trees desired for wildlife plantings. When the nursery is in full operation it will produce 10 million to 12 million trees annually. At the present time, the Department is using inmate labor from a nearby honor prison camp.

Stinchfield Woods.--This tract of 840 acres consists of both native oak woodland and extensive areas of old fields now planted to various conifers. White pine, Norway spruce, and Austrian pine have been the most successful planted species. A major point of interest here was the comparative development of Scotch pine of Bavarian, Norwegian, and Riga origins planted in 1930 and 1933.

Newcomb Tract.--This tract of 206 acres across the Huron River to the east of the Stinchfield Woods tract, occupies a similar site. The School of Natural Resources maintains a small experimental nursery at the residence on the tract and is utilizing the large field across the road for provenience trials. Of primary interest here were nursery beds including 24 proveniences of European larch and 1 each of Japanese and Dunkeld larches, and a field planting of 3 sources of European and 1 source of Japanese larch.

1/ Arranged by F. J. Hodge, in charge of nurseries and planting in the Forestry Division, Michigan Conservation Department, and S. H. Spurr, Professor of Silviculture, School of Conservation, University of Michigan.

Saginaw Forest.--Acquired in 1903, this 80-acre tract near Ann Arbor has now been largely planted. A wide variety of both conifer and hardwood plantations dating from 1904 have been managed intensively with thinnings, plot measurement, and photographs at 5-year intervals. Of special interest here was the comparative development of many tree species including some of the oldest successful hardwood plantations in this region.

LIST OF THOSE REGISTERED AT THE CONFERENCE

Name — Address

Clifford E. Ahlgren, Quetico-Superior Wilderness Research Center, Ely, Minn.

Dow Baxter, School of Natural Resources, University of Michigan, Ann Arbor, Mich.

Stephen G. Boyce, Central States Forest Experiment Station, Carbondale Research Center, Box 760, Carbondale, Ill.

R. A. Brink, Department of Genetics, University of Wisconsin, Madison 6, Wis.

Ira Bull, Department of Forestry, Michigan State University, East Lansing, Mich.

Edward D. Clifford, U.S. Forest Service, Wellston, Mich.

Dr. W. H. Cram, Forest Nursery Station, Canada Department of Agriculture, Indian Head, Saskatchewan

Maurice W. Day, Dunbar Forest Experiment Station, Sault Ste. Marie, Mich.

D. W. Einspahr, Institute of Paper Chemistry, Appleton, Wis.

Stanley G. Fontanna, School of Natural Resources, University of Michigan, Ann Arbor, Mich.

Harry A. Fowells, Division of Forest Management Research, Forest Service, USDA, Washington 25, D.C.

David T. Funk, Central States Forest Experiment Station, Athens Ohio Research Center, P.O. Box 475, Athens, Ohio.

John B. Genys, Department of Forestry, Michigan State University, East Lansing, Mich.

Richard M. Godman, Lake States Forest Experiment Station, East Lansing Research Center, Cadillac, Mich.

John Grafius, Department of Farm Crops, Michigan State University, East Lansing, Mich.

R. R. Hartig, Genetics Department, University of Wisconsin, Madison 6, Wis.

James A. Herman, Buskirk Lumber Co., Sandusky, Mich.

F. J. Hodge, Forestry Division, Michigan Department of Conservation, Lansing, Mich.

Victor Horvath, 812 Duncan Street, Ann Arbor, Mich.

John Hosner, Forestry Department, Southern Illinois University, Carbondale, Ill.

J. J. Jokela, Department of Forestry, University of Illinois, Urbana, Ill.

M. Sulaiman Kakli, University of Michigan, Ann Arbor, Mich.

M. Kaye, Room 7, 469 Broadway Avenue, Winnipeg 1, Manitoba

William C. Kennard, State Experiment Stations Division, USDA, Washington 25, D.C.

H. B. Kriebel, Ohio Agriculture Experiment Station, Wooster, Ohio

James E. Kuntz, Department of Plant Pathology, University of Wisconsin, Madison 6, Wis.

James Lamy, Abitibi Corporation, Alpena, Mich.

Philip R. Larson, Lake States Forest Experiment Station, Northern Institute of Forest Genetics, Star Route #2, Rhinelander, Wis.

E. N. Lee, North Central Region, U.S. Forest Service, 710 N. Sixth Street, Milwaukee 3, Wis.

G. A. Limstrom, Central States Forest Experiment Station, 111 Old Federal Building, Columbus 15, Ohio

Richard Lohrey, Lake States Forest Experiment Station, East Lansing Research Center, Cadillac, Mich.

J. W. Macon, Consolidated Water Power & Paper Co., Box 381, Rhinelander, Wis.

Hans Nienstaedt, Lake States Forest Experiment Station, Northern Institute of Forest Genetics, Star Route #2, Rhinelander, Wis.

Les Olmstead, Michigan Department of Conservation, Lansing, Mich.

Robert F. Patton, Department of Plant Pathology, University of Wisconsin, Madison 6, Wis.

Maxon Y. Pillow, Forest Products Laboratory, Madison 5, Wis.

William J. Potter, School of Natural Resources, University of Michigan, Ann Arbor, Mich.

Ralph A. Read, Rocky Mountain Forest and Range Experiment Station, Lincoln Research Center, College of Agriculture, Lincoln, Neb.

John L. Ruby, Department of Forestry, Michigan State University, East Lansing, Mich.

Paul O. Rudolf, Lake States Forest Experiment Station, St. Paul 1, Minn.

Tom Rudolph, Lake States Forest Experiment Station, Northern Institute of Forest Genetics, Star Route #2, Rhinelander, Wis.

C. A. Samuelson, 504 W. Magnetic Street, Marquette, Mich.

Ernst J. Schreiner, Northeastern Forest Experiment Station, Morris Arboretum, Philadelphia 18, Pa.

Grant Sharpe, 1230 Saunders Crescent, Ann Arbor, Mich.

Norman Smith, Michigan Department of Conservation, Lansing, Mich.

Stephen H. Spurr, School of Natural Resources, University of Michigan, Ann Arbor, Mich.

Erich Steiner, Department of Botany, University of Michigan, Ann Arbor, Mich.

J. P. Van Buijtenen, Institute of Paper Chemistry, Appleton, Wis.

Osborn O. Wells, Forestry Department, Michigan State University, East Lansing, Mich.

G. C. Warrack, Apt. 108, 721 S. Forest, Ann Arbor, Mich.

Jonathan W. Wright, Forestry Department, Michigan State University, East Lansing, Mich.

COMMON AND SCIENTIFIC NAMES OF TREE GENERA AND SPECIES MENTIONED IN TEXT[1/]

Common Name	Scientific Name
Alder, Caucasian	*Alnus subcordata*
Alder, Italian	*A. cordata*
Aspen, bigtooth	*Populus grandidentata*
Aspen, European	*P. tremula*
Aspen, quaking	*P. tremuloides*
Beefwood	*Casuarina*
Birch	*Betula*
Birch, paper	*B. papyrifera*
Birch, European white	*B. pendula*
Beech, American	*Fagus grandifolia*
Beech, European	*F. sylvatica*
Chestnut, American	*Castanea dentata*
Chestnut, Chinese	*C. mollissima*
Chestnut, Japanese	*C. crenata*
Coconut	*Cocos nucifera*
Douglas-fir	*Pseudotsuga menziesii*
Elm	*Ulmus*
Elm, American	*Ulmus americana*
Eucalyptus	*Eucalyptus*
Eucalyptus, Tasmanian blue	*E. globulus*
Fir, balsam	*Abies balsamea*
Fir, grand	*A. grandis*
Hemlock, eastern	*Tsuga canadensis*
Larch, Dunkeld	*Larix eurolepis*
Larch, European	*L. decidua*
Larch, Japanese	*L. leptolepis*
Larch, western	*L. occidentalis*
Locust, black	*Robinia pseudoacacia*

1/ Authorities for nomenclature are: Check List of Native and Naturalized Trees of the United States, by Elbert L. Little, USDA Agr. Handb. 41, 1953; and Standardized Plant Names, by Harlan P. Kelsey and William A. Dayton, 1942, Harrisburg, Pa.

Mahogany	Swietenia
Maple, sugar	Acer saccharum
Oak, Caucasian	Quercus macranthera
Oak, English	Q. robur
Oak, northern red	Q. rubra
Pine Austrian	Pinus nigra
Pine, Balkan	P. peuce
Pine, Caribbean	P. caribaea
Pine, cluster	P. pinaster
Pine, Coulter	P. coulteri
Pine, eastern white	P. strobus
Pine, European black (See Austrian pine)	
Pine, Himalayan	P. griffithi
Pine, jack	P. banksiana
Pine, Japanese black	P. thunbergi
Pine, Japanese red	P. densiflora
Pine, Jeffrey	P. jeffreyi
Pine, Jelecote	P. patula
Pine, knobcone	P. attenuata
Pine, loblolly	P. taeda
Pine, lodgepole	P. contorta
Pine, limber	P. flexilis
Pine, Monterey	P. radiata
Pine, pitch	P. rigida
Pine, ponderosa	P. ponderosa
Pine, red	P. resinosa
Pine, Scotch	P. sylvestris
Pine, shortleaf	P. echinata
Pine, slash	P. elliottii
Pine, sugar	P. lambertiana
Pine, western white	P. monticola
Pine, whitebark	P. albicaulis
Poplars	Populus
Rubbertree	Hevea
Spruce, black	Picea mariana
Spruce, Engelmann	P. engelmannii
Spruce, Norway	P. abies
Spruce, red	P. rubens
Spruce, Serbian	P. omorika
Spruce, Sitka	P. sitchensis
Spruce, white	P. glauca
Teak, common	Tectona grandis
White-cedar, northern	Thuja occidentalis

LIST OF PUBLICATIONS PREVIOUSLY ISSUED
FOR THE
LAKE STATES FOREST TREE IMPROVEMENT COMMITTEE

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Proceedings, Lake States Forest Tree Improvement Conference, August 30-31, 1955. Lake States Forest Expt. Sta. Misc. Rpt. 40, 108 pp., illus. (Processed.) 1955.

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Guide for Selecting Superior Trees and Stands in the Lake States, by Paul O. Rudolf. Lake States Forest Expt. Sta., Sta. Paper 40, 32 pp., illus. (Processed.) 1956.

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Registering and Marking Selections in the Lake States; A Report of a Subcommittee of the Lake States Forest Tree Improvement Committee, by Paul O. Rudolf and H. E. Ochsner. U.S. Forest Service, North Central Region (no series), 9 pp. (Processed.) 1959.

Forest Tree Seed Certification in the United States; A Report of a Subcommittee of the Lake States Forest Tree Improvement Committee, by J. W. Macon. Consolidated Water Power & Paper Co. (no series), 3 pp. (Processed.) 1959.

SOME RECENT STATION PAPERS
Lake States Forest Experiment Station

Incidence of White Pine Blister Rust Infection in the Lake States, by D. B. King. Sta. Paper 64, 12 pp., illus. 1958.

Fire Fuels in Red Pine Plantations, by Loyd LaMois, Sta. Paper 68, 19 pp., illus. 1958.

Snow Behavior in Forests of Northern Minnesota and its Management Implications, by Sidney Weitzman and Roger R. Bay. Sta. Paper 69, 18 pp., illus. 1959.

Growth of Swamp Conifers Following an Improvement Cut, by D. D. Skilling. Sta. Paper 71, 10 pp., illus. 1959.

Direct Seeding and Planting of Balsam Fir in Northern Wisconsin, by J. H. Stoeckeler and D. D. Skilling. Sta. Paper 72, 22 pp., illus. 1959.

Wood Use by Manufacturing Firms in Minneapolis and Saint Paul, by John R. Warner and Carl H. Tubbs. Sta. Paper 75, 30 pp., illus. 1959.

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